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PHOTOPERIOD, GENOTYPE, AND NUTRITIONAL INFLUENCES ON REPRODUCTIVE EFFICIENCY OF FEMALE BROILER BREEDERS

by

NANCY SUSAN JOSEPH

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Photoperiod, Genotype, and Nutritional Influences on Reproductive Efficiency of Female Broiler Breeders submitted by Nancy Susan Joseph in partial fulfilment of the requirements for the degree of Master of Science in Animal Science.

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ABSTRACT

As genetic selection for increased broiler breast muscle yield and growth rate continue the management techniques of broiler breeder flocks are routinely redefined. The effects of strain, crude protein (CP) intake (Experiment 1), age at photostimulation (Experiment 2), and a mid-cycle increase in photoperiod (Experiment 3) were studied in broiler breeder hens. A difference of 14 versus 16% dietary CP can result in a decrease in egg size and egg production. Photostimulating a flock at 23 versus 20 weeks of age did not decrease egg production. A strain selected for increased breast muscle yield had an increase in ovary weight at 53 weeks of age when photostimulated at 23 weeks of age. A mid-cycle increase in daylength did not alter the rate of egg production or ovarian morphology in breeder hens. Improved flock performance was associated with reducing the variability in body weight before reproductive development began.

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ABBREVIATION KEY

A bird	bird that was processed prior to photostimulation
AME	apparent metabolizable energy
B bird	bird that was processed after sexual maturation, specifically after the third oviposition
BW	body weight
C bird	bird that was processed after a defined period in lay
C-32 bird	bird that was processed at 32 wk of age
C-40 bird	bird that was processed at 40 wk of age
C-54 bird	bird that was processed at 54 wk of age
CP	crude protein
d	day(s)
EXP	Arbor Acres experimental strain selected for high breast muscle yield
FSH	follicle stimulating hormone
FSY	Arbor Acres Feather Sexable Yield
F1	LYF on the ovary with the highest weight
GnRH	gonadotropin releasing hormone
h	hour(s)
LH	luteinizing hormone
LYF	large yellow follicle(s); greater than 10 mm in diameter
ME	metabolizable energy
NRC	National Research Council
RIA	radioimmunoassay
PS	photostimulation
SM	sexual maturity
SYF	small yellow follicle(s); 5 to 10 mm in diameter
WF	white follicle(s); less than 5 mm in diameter
wk	week(s)
14L:10D	14 hours of light and 10 hours of darkness per day
18L:6D	18 hours of light and 6 hours of darkness per day

1.0 INTRODUCTION

1.1 BACKGROUND

The Hatching Egg Industry

The poultry industry is one that is large and highly specialized, designed to meet the needs of the consumer. For example, the table egg industry, as the name would imply, produces eggs destined for human consumption. Likewise, in the broiler industry, the finished product ends up in the meat section of the supermarket. Getting to the final stage of production requires multiple generations of genetic selection for the trait most desirable for that industry. For the meat-type market, chickens are selected for appetite and growth resulting in a carcass with maximized meat yield. In this industry, companies have multiple genetic populations of birds that they use to create the chicken that the consumer desires. These primary breeder companies provide farmers with parent or broiler breeder chickens. At this stage it becomes the producer's responsibility to provide fertilized eggs that hatch into broilers destined for the processing plant. At this level of production, farmers are known as hatching egg producers.

The Current Situation in Canada

It would seem that once the hatching egg producer receives the parent stock from the primary breeder company that raising and caring for these birds would be straightforward, but it is not. Birds are heavily selected for appetite in order to encourage rapid growth. A desirable trait to the broiler producer but not to the hatching egg producer. Genetic selection for increased food consumption has adversely affected the reproductive qualities of the broiler breeder (Siegel and Dunnington, 1985). Obesity, associated with increased feed consumption, results in increased body weight, which leads to poorer egg production, fertility, and hatchability (Marks, 1985). As such, broiler breeders have to be feed restricted to control energy intake, thereby controlling body weight. Some of the biggest issues in the hatching egg industry are the appropriate level of feed restriction, body size and composition, egg production, fertility, and hatchability of eggs set. In

1998, close to 700 million broiler eggs were set in registered hatcheries across Canada. Therefore, resolving some of these issues would benefit a large sector of the broiler industry. Applied scientific studies are aimed at trying to maximize the reproductive potential of these birds through the use of lighting programs, nutrition, housing methods and immunology. This thesis described experiments in which effects of photoperiod were studied both early in lay (i.e. prior to sexual maturation) and after peak egg production. As well, the effects of dietary crude protein level on the pullet to layer transition period were also determined.

1.2 PHOTOPERIODISM AND REPRODUCTIVE PHYSIOLOGY OF THE FEMALE BROILER BREEDER

Some mammalian and avian species in temperate climates mate seasonally. For these animals, conception is restricted to a specific time of the year commonly termed the breeding season. Day length is the single most important environmental cue that essentially controls the onset and length of the breeding season. This physiological mechanism exists because survival of the offspring will be optimal at a time of year when environmental temperatures are high and food is abundant (eg. spring and summer). Therefore, the optimal breeding season for each species is going to differ. For example, sheep are known as 'short-day' breeders, that is, decreasing day lengths after the summer solstice signals the approaching fall and winter and consequently initiates the breeding season. Lambing thus occurs in late winter / early spring (Foster et al., 1986). Alternatively, chickens are 'photostimulated' by the increasing day lengths of spring and summer (Farner, 1964). The actual length of the reproductive period is relatively short and the rest of the year is termed the anestrus season as the female is relatively anovulatory (Foster et al., 1986). This eliminates the possibility of producing offspring during a season when conditions are less favorable. In order for light to induce a photoperiodic response, the animal must first perceive day length. Then the neural impulse that is created must then be translated into an neuroendocrine signal that will either stimulate or inhibit reproductive function. The next two sections will cover the perception of light and the stimulation of the reproductive axis by light.

The Perception of Light

The perception and transmission of light in birds is one that is taken for granted yet poorly understood. Light was believed to be perceived through the retina for purposes of reproduction, however, the work of Benoit (1964) clearly demonstrated that light perception controlling reproduction in birds occurs primarily through the hypothalamus, with the eye acting as a superficial photoreceptor. Further studies revealed similar findings.

Ali and Cheng (1985) used genetically sighted and blind female chickens to compare their rate of egg production after photostimulation. Sexual maturation occurred in the blind birds in response to photostimulation and they had a higher rate of egg production than the sighted hens. Like Ali and Cheng (1985), Siopes and Wilson (1980) compared the photosexual response of ocularly blind and intact domestic chickens to either incandescent or fluorescent light. Blind hens showed reproductive development. There were no differences in egg production between blind and sighted chickens under fluorescent lighting. Incandescent lighting, however, had an inhibitory effect on the egg production in ocularly intact chickens. Therefore, Siopes and Wilson (1980) concluded that although the eyes were not essential for sexual development, they were capable of altering the photoperiodic response. The hypothalamic or deep photoreceptors, however, were essential for perceiving light.

Homma et al. (1980) studied the perception of light by deep photoreceptors in the brain. Radioluminous beads were implanted into various regions of the brain to emit visible light (either blue or orange-yellow). Under a short day photoperiod (8 hours of light/day), sexually immature Japanese quail receiving radioluminous beads exhibited testicular growth as compared to those that had either plastic beads implanted into their brain or no implantation. Also, when radioluminous beads were implanted behind the eyeball and close to the hypothalamus, the quail experienced a strong gonadal stimulation. This too, suggested that the deep photoreceptors of the hypothalamus were more involved in transmitting the photoperiodic response than the eye (Homma et al., 1980). However discovery of the hypothalamic photoreceptors, and the possibility of photoreceptors in the pineal gland continued to elude researchers.

The Pathways of Light Transmission. The avian system of light transmission involves a complex network of receptors and oscillators. Part of the difficulty in determining this network was that avian physiologists had not deciphered the pathway of light transmission. The three possible sites where photoreceptors may have induced a neuroendocrine reproductive response were the retina, the pineal gland, and the ventral forebrain (Kuenzel, 1993). As mentioned earlier, several studies had already demonstrated that the retina was not needed to elicit a reproductive response (Ali and Cheng, 1985; Siopes and Wilson, 1980; Homma et al., 1980). The pineal gland contains cells, known as pinealocytes that develop from primary photoreceptors (Oksche, 1980). These pinealocytes contain indoleamines capable of synthesizing melatonin from serotonin (Oksche, 1980). Lynch and Ralph (1970) noted that a diurnal pattern in melatonin secretion existed in both chickens and Japanese quail. The amount of melatonin secretion during the night was almost 20 times greater than it was during the day. Also, increased mRNA levels of the enzymes required in the melatonin synthesis pathway were noted during the dark phase in the chick pineal gland (Sun et al., 1993; Bernard et al., 1997; Bernard et al., 1999). As pinealocytes are derived from photoreceptors, and are capable of synthesizing melatonin in response to a circadian rhythm, Nakahara et al. (1997) suggested that the pineal gland possessed the ability to perceive light and directly transform the photic information into a measure of day length.

Unfortunately, the relationship between day length, melatonin, and reproduction has not been clearly described in avian species. There are two possible explanations for the lack of a concise role for the pineal gland. One is that pinealectomy in chickens (Harrison and Becker, 1969), Japanese quail (Homma et al., 1967) and house sparrows (Menaker et al., 1970) does not abolish gonadal development under stimulatory lighting regimes. This is most likely because there are melatonin producing cells in the retina and other brain areas of the bird (Quay, 1965; Paug et al., 1977; Binkley et al., 1979; Iuvone, 1990) and retinal production of melatonin, like that of the pineal, follows a circadian rhythm (Binkley et al., 1979; Hamm and Menaker, 1980; Iuvone, 1990). Even after pinealectomy, Hamm and Menaker (1980) demonstrated that the pattern of retinal N-acetyltransferase, an enzyme used to synthesize melatonin, persists in a circadian manner. The second explanation is the existence of other photoreceptors besides the ones located in the retina and pineal, as Benoit (1964) had originally postulated. Implantation of radioluminous material into the infundibular nuclear complex of the mediobasal hypothalamus resulted in gonadal recrudescence in ducks, white-crowned sparrows, and Japanese quail (Oliver and Bayle, 1976; 1982; Oliver et al., 1979). Photoreceptors contained the rhodopsin photopigment, which absorb photons, the first step in transmitting visual information. Silver et al. in 1988 located cerebrospinal fluid-contacting neurons within the infundibular complex that showed immunoreactivity to visual pigment antibodies specific to rhodopsin.

Although the precise location of the encephalic photoreceptors has not been deciphered, it is certain that these photoreceptors mediate reproductive development and involution in response to changes in day length. The process of ovarian development, sexual maturation, and estrous cyclicity is discussed below.

Photoperiod and the Hypothalamo-Pituitary-Ovarian Axis

Chickens interpret a change in photoperiod as a change in the seasons that govern the reproductive cycle. Although the mechanism by which chickens measure day length is still unclear, it is certain that this mechanism allows the bird to accurately time the breeding season and, subsequently, the anestrous season. For chickens, responding to an increase in day length involves initiating a series of physiological events that lead to sexual maturation and ovulatory cyclicity. The reproductive components that are involved in regulating hormonal activity are collectively known in the female bird as the hypothalamo-pituitary-ovarian axis (Scanes, 1984). The hypothalamus is considered to be the master endocrine gland that controls the other reproductive components in the body. The hypothalamus secretes gonadotropin-releasing hormone (GnRH), which then travels to the anterior pituitary or adenohypophysis via the hypophysial portal pathway. The release of GnRH stimulates the adenohypophysis to secrete two gonadotropins, luteinizing hormone (LH) and follicle-stimulating hormone (FSH). The gonadotropins bind to receptor sites on the ovary and stimulate the production of ovarian steroids, follicular maturation, and ovulation.

Ovarian Development and Sexual Maturation. Gilbert (1971) outlined the development of the ovary from hatching to sexual maturation. Briefly, as early as 3 days of incubation, the ovary begins to form in the female chick. At this time, primordial germ cells and mesenchymal cells are incorporated into the germinal epithelium. The primary sex cords form between day 6 and 7 of incubation. During days 8 to 11, the germinal epithelium forms the ovarian cortex and secondary sex cords. Oogonia appear and multiply by mitotic division until hatching. This early stage of gonadal development is not under the control of the hypothalamus or pituitary but rather controlled by the ovarian steroid hormones that are produced beginning at days 2 to 6 of incubation. Upon hatching, the oogonia, referred to as oocytes, remain in an arrested state of development until sexual maturation occurs. Both ovaries are present in the female when the chick hatches, however, the germinal epithelium in the right ovary fails to develop into the ovarian cortex. As a result, at about 3 weeks post-hatch, the primordial germ cells of the right ovary regress and disappear. This process is believed to be caused by the early onset of estrogen production by the left ovary (Gilbert, 1971).

Sexual maturation was defined by Gilbert (1971) as the morphological and physiological changes in the body that culminate in the reproductive capability of the animal. The most common measurement of sexual maturity is the age at which the first oviposition occurs. Although birds eventually become sexually mature under short day lengths, an increase from a short to long day length advances the onset of lay (Morris et al., 1964). This effect is mediated by the hypothalamo-pituitary-ovarian axis. ~~The~~ hypothalamus stimulates the secretion of gonadotropins from the anterior pituitary by secreting a neurohormone via a portal system that connects the two structures (Fraps, 1961). Early studies demonstrated that, like mammals, the neurohormone GnRH stimulates ovarian development and ovulation in fowl (Reeves et al., 1973; van Tienhoven and Schally, 1973; Bonney et al., 1974). Chickens have two forms of GnRH, known simply as GnRH-I and GnRH-II (King and Millar, 1982; Miyamoto et al., 1982; Miyamoto et al., 1984). Dunn and Sharp (1999) found that GnRH neurones respond to photostimulation by increasing GnRH-I gene transcription. Therefore GnRH-I is believed to be more physiologically important than GnRH-II (Sharp et al., 1990).

Bullock and Nalbandov (1967) first suggested that LH secretion from the anterior pituitary is under the humoral control of the hypothalamus. Changes in the concentration of plasma LH reflect changes in the stage of follicular maturation and ovulation in the ovary. Although LH is present in the circulation of juvenile birds, the concentration is quite low (Scanes et al., 1978; Scanes et al., 1980). Wilson and Sharp (1975) noted that prior to sexual maturity, there is an increase in plasma LH concentration. This pre-pubertal rise in LH is believed to be caused by a desensitization of the ovarian steroid negative feedback system that maintained LH concentration at basal levels (Wilson and Sharp, 1975). During the final stage of reproductive development, rapid growth of the large yolky follicles occurs corresponding to an increase in progesterone concentration and activation of the progesterone positive feedback mechanism. After sexual maturity, the negative feedback effects of estradiol and the positive feedback effects of progesterone work in concert to regulate estrous cyclicity.

Gilbert et al. (1983) noted that once reproductive development is initiated, follicular growth is a continuous process. The growth phase for a follicle is: from 3 to 5 mm, 3 days; from 5 to 8 mm, 2 days; from 8 mm to ovulation, 6 days; for a total of 11 days from 3 mm to an ovulable state (Gilbert, 1971). Ovarian follicles can be classified according to their size (Robinson and Etches, 1986). All follicles begin as small white follicles (SWF), which are less than 1 mm in diameter. Large white follicles (LWF) are between 2 to 5 mm in diameter. These follicles are described as being 'white' because of the paleness of the yolk material (Gilbert and Wells, 1984). Once the rapid accumulation of yellow yolk occurs the follicles are referred to as either small yellow follicles (SYF) measuring 5 to 10 mm in diameter or large yellow follicles (LYF) that are greater than 10 mm in diameter. Williams and Sharp (1978a) stated that there are usually between 5 to 7 LYF at any given time in a broiler breeder hen. The LYF are arranged in a hierarchy, with the largest follicle (F1) ovulated first and the second largest (F2) ovulated the second day, the third largest (F3) ovulated the next day (Bahr and Johnson, 1984). Once the F1 follicle ovulates, which occurs every 25 to 28 hours, the next mature follicle (i.e. F2) moves up to the first position in the hierarchy with each successive follicle also advancing one position (Bahr and Johnson, 1984). With each follicle that ovulates, there are approximately 20 follicles that do not (Romanoff and Romanoff, 1949). Yet this only represents a small fraction of the total number of follicles in the ovary (Romanoff and Romanoff, 1949). Therefore the hen produces more oocytes than is needed, eliminating the excess by atresia. Atresia is the process whereby follicles stop growing and regress. An atretic follicle is characterized by the presence of small hemorrhages on the surface and a deformed or shrunken appearance (Gilbert et al., 1983). The incidence of atresia is greatest among the smallest follicles (i.e. SWF and LWF) (Gilbert et al., 1983). This process serves to decrease the number of follicles with each successive class size. Very little atresia normally occurs in the larger sized follicles, so once a follicle enters the hierarchy it is typically ovulated. One of the more intriguing aspects of the ovarian hierarchy is the orderly maturation of the pre-ovulatory follicles. The mechanisms that regulate the hierarchy most likely involve the steroid production by the follicles themselves.

Ovarian Steroidogenesis. The wall of a mature follicle consists of six layers: the vitelline membrane, the perivitelline and granulosa layer, the theca interna, the theca externa, connective tissue, and finally, the germinal epithelium (Gilbert, 1971). These layers interact to support the follicle, to aid in growth and maturation, culminating in ovulation. The theca and granulosa layers, for example, are responsible for the production of ovarian steroids. The granulosa cells synthesize progesterone. LH promotes steroid hormone production in the follicular cells (Hammond et al., 1980). Incubation of granulosa cells (taken from an F1 follicle) in ovine LH cause an increase in the concentration of progesterone *in vitro* (153.5 ± 34.2 pmol/ug DNA compared to the basal level of 62.3 ± 34.4 pmol/ug DNA) (Wells et al., 1980). In turn, the theca cell layer is responsible for synthesizing estrogens and androgens (Huang et al., 1979; Bahr et al., 1983; Robinson and Etches, 1986).

Shahabi et al. (1975) found that among the three largest pre-ovulatory follicles, the F1 synthesized the most progesterone while the F3 seemed to only synthesize estrogen. It was later realized that the production of estrogen and progesterone within a follicle is dependent on it's stage of maturity (Huang et al., 1979). Huang et al. (1979) postulated a two cell – two hormone model to describe the relationship between granulosa and theca cells. In the immature pre-ovulatory follicle, progesterone, produced in the granulosa cells, is metabolized to androgens in the theca cells. The theca cells then create estrogen from aromatizing the androgens; thus estrogen concentration increases while progesterone concentration decreases (Huang et al., 1979). *In vitro* measurements of aromatase activity confirm that the theca cells produce estrogen from testosterone (Wang and Bahr, 1983). However, Robinson and Etches (1986) demonstrated that the ability to convert progesterone to androgens such as testosterone was lost once the follicle assumed the F1 position. Armstrong (1985) discovered that follicles weighing as little as 1 mg exhibit aromatase activity and Robinson and Etches (1986) found that androstenedione, dehydroepiandrostenedione, and estradiol are produced by the small follicles and that this steroidogenesis could be stimulated *in vitro* by LH. The level of aromatase activity and the concentrations of the steroid hormones increase as the follicle progresses from the SWF to SYF stage (Armstrong, 1985; Robinson and Etches, 1986). Therefore, the principle source of estrogen is the small follicles. However, once a follicle reaches the SYF state, aromatase activity begins to decline (Armstrong, 1985). Yu et al. (1992) found that the production of estradiol from the five largest follicles is less than 2.5 ng per follicle during a 3-hour *in vitro* incubation.

The Ovulatory Cycle. LH is responsible for inducing ovarian steroidogenesis and stimulating ovulation (Wilson and Cunningham, 1984). The secretion of LH is under the hypothalamic control of GnRH (Wilson and Sharp, 1975; Etches and Cunningham, 1975). Etches and Cunningham (1975; 1976) demonstrated that ovulation could be induced prematurely by injecting physiological levels of GnRH into hens. There are two different patterns of LH concentrations in the plasma during the ovulatory cycle. The first is a tonic LH secretion that follows a diurnal rhythm (Wilson and Cunningham, 1984). At the onset of darkness, the tonic level of LH increases marginally and then declines until approximately 14 hours after the onset of darkness, when it increases again. The cyclic pattern of plasma LH concentration involves a single maximal increase, 4 to 7 hours before ovulation, termed the preovulatory LH surge (Furr et al., 1973; Wilson and Sharp, 1973).

This surge is an obligatory condition for ovulation to occur. The first ovulation in a sequence occurs shortly after the onset of light or daybreak with each successive ovulation occurring at a later time each day. The sequence is completed with a terminal ovulation that typically occurs in the afternoon (Fraps, 1961). Termination of one sequence is usually followed by the initiation of another, 40-44 hours after the last ovulation. It was Fraps (1954) that first postulated that ovulation only occurred within an 8 hour period of the day termed the 'open period'. The term has been modified to the period during which the preovulatory LH surge occurs, referred to as the 'open period for LH release.'

Changes in the concentrations of ovarian hormones serve to stimulate the preovulatory rise in LH (Wilson and Cunningham, 1984). Plasma estrogen concentration reaches peak levels approximately 18 hours before ovulation while progesterone concentration does not increase until 8 hours before ovulation (Wilson and Cunningham, 1984). The rise in progesterone concentration stimulates a rise in LH concentration, which in turn stimulates a further rise in progesterone. This positive feedback loop is what causes the LH surge (Johnson et al., 1985). Progesterone primarily targets receptor sites in the hypothalamus (Wilson and Cunningham, 1984). The peak concentration of progesterone receptors on both the hypothalamus and the pituitary occurs 8 hours before ovulation, coincident with the time that progesterone is at maximal levels in the plasma and just before the LH surge is expected to happen (Kawashima et al., 1979).

Progesterone can not induce the LH surge unless the hen has sufficient concentrations of both estrogen and progesterone in the blood. Injecting either progesterone alone or estrogen alone into ovariectomized hens failed to induce the preovulatory LH surge, however, when the hen received both steroids, estrogen followed by progesterone, plasma LH concentration increased (Wilson and Sharp, 1976). Presumably the role of estrogen is to facilitate the effect of progesterone on the hypothalamus and anterior pituitary. Kawashima et al. (1979) found that estrogen stimulated the production of progesterone receptors on the hypothalamus and pituitary. Bonney and Cunningham (1977) injected sexually immature hens with progesterone, testosterone and estradiol and found that those injected with estradiol exhibited a strong LH response to an injection of GnRH. Kawashima et al. (1993) measured the amount of estrogen receptor binding during the ovulatory cycle and noted that changes in estrogen receptor concentration preceded changes in progesterone receptor binding.

Photoreceptors serve to mediate the reproductive response to a change in day length. What is still unknown is the precise location of these photoreceptors and how they work with circadian oscillators to accurately time the light and dark phases of the day. What is known is that once a pullet is photostimulated, sexual maturation ensues. The next section examines how differences in age at photostimulation can affect the timing of puberty, body composition, egg size, and the rate of egg production.

1.3 THE EFFECTS OF AGE AT PHOTOSTIMULATION ON REPRODUCTIVE PERFORMANCE

Photostimulation refers to the process by which the increasing photoperiods of spring and summer stimulate reproductive development in the chicken (Farner, 1964). Domestic chickens do not respond to a given photoperiod in the same way as their counterparts do in the wild. Photoperiod can affect the rate at which sexual maturation occurs and the rate of egg production in chickens but it does not initiate or terminate reproductive function (Morris, 1967). Studies have shown that sexual maturity can proceed without photostimulation. Birds that are reared in total darkness eventually start laying (King, 1961; 1962). Also, birds that are laying under a stimulatory photoperiod continue to lay for up to 5 weeks in complete darkness (Wilson and Woodard, 1958). Therefore, the role of photostimulation is to modify the timing of reproductive development. Morris and Fox (1958) and Morris et al. (1964) postulated that the rate of sexual maturity is influenced more by the change in photoperiod than by the absolute length of a given photoperiod. At a constant 6, 14, or 22 hours of light/day, the rate of egg production was similar among birds (Morris et al., 1964). However, when the photoperiod was increased (i.e. from 6 to 14 hours or 14 to 22 hours of light/day), rates of egg production increased above rates for constant day lengths. When the photoperiod was decreased (i.e. from 14 to 6 hours or 22 to 14 hours of light/day), the rate of lay also decreased. Morris et al. (1964) concluded that there was no single 'optimum' day length for egg production; rather egg production increased when photoperiod increased.

All of the components needed to elicit a photo-induced reproductive response are present in juvenile birds (Sharp, 1992). However exposure to long day lengths early in the bird's life actually delays sexual maturation (Sharp, 1992). In windowless houses, day length is controlled artificially by using indoor light sources on a pre-determined photoschedule. Therefore the chicks hatched and reared indoors are not even aware that the natural day length is changing. A successful lighting program is one that maximizes settable egg production within the flock. In order for this to occur, it is necessary for the lighting program to stimulate sexual maturation at the right age. The effect of age at photostimulation on age at sexual maturation and other reproductive characteristics is discussed.

Age at Sexual Maturity and Body Weight Uniformity

Sexual maturation, defined as age at first egg, is dependent on achieving minimum thresholds of age, body weight, and body composition (Brody et al., 1984; Zelenka et al., 1986; Katanbaf et al., 1989). For meat-type birds, with *ad libitum* access to feed, the rate-limiting factor for the onset of lay is age, because the requirements for body weight and body composition have been met (Katanbaf et al., 1989). However when meat-type birds have restricted access to feed, a common practice in the hatching egg industry, mature BW and body composition become the requirements for sexual maturation (Leeson and Summers, 1983; Soller et al., 1984; Katanbaf et al., 1989). Therefore, there is no advantage to photostimulating a broiler breeder flock too early, as sexual maturity will not be advanced in these feed restricted birds. A successful lighting program will stimulate sexual maturation when the BW and body composition requirements have been met. Yuan et al. (1994) found that age at first oviposition was delayed by 2 weeks when broiler breeders were photostimulated at 20 weeks of age as compared to 14 or 17 weeks of age. However, photostimulating at 14 weeks of age proved to be too early as these birds took just as long to reach sexual maturity as those that were photostimulated at 17 weeks of age. Likewise, Robinson et al. (1996) found that photostimulating broiler breeders at 120 versus 140 days of age did not result in earlier sexual maturity. Therefore delaying photostimulation is beneficial as it allows more time for the bird to attain an appropriate body size. Broiler breeders require more time for sexual maturity, unlike egg layers that are getting younger at sexual maturity. For every day earlier that Leghorn pullets were photostimulated, age at sexual maturity was decreased by 0.44 days (Leeson et al., 1988). Genetic selection for egg production in layer stock has contributed to this effect (Ernst et al., 1987). Unfortunately, the opposite is occurring in broiler stock, in which the onset of lay is being pushed further back (Yuan et al., 1994).

Robinson et al. (1996) noted that when birds were photostimulated at 160 days of age sexual maturity was delayed, however the number of days between photostimulation and sexual maturity was significantly reduced. This also correlated with a decrease in the variability in body weight at sexual maturity. Another characteristic was that hens photostimulated at 150 or 160 days of age had a higher percentage of carcass lipid at sexual maturity than hens photostimulated at 120, 130, or 140 days of age (Robinson et al., 1996). Brody et al. (1984) noted that hens at sexual maturity had larger abdominal fat pads than pullets. Increasing the age at which photostimulation occurs in egg-layers was also related to an increase in body fat and a decrease in protein (Leeson et al., 1988). This indicated that beyond achieving a minimum age requirement, the onset of sexual maturity is also dependent on reaching a threshold body weight and a threshold level of carcass fat. The birds photostimulated at 160 days of age had a larger girth than birds photostimulated at younger ages (Robinson et al., 1996). The girth measurement corresponds to the degree of fleshing on the bird and indicates that birds photostimulated later had a more mature frame size. In contrast, the early-photostimulated birds (120 days of age) had the smallest girth and keel at photostimulation, indicating that they were still undergoing skeletal growth. Robinson et al. (1996) concluded that as birds age, less skeletal growth occurs as energy from feed intake is diverted into tissue accretion – particularly into fat deposition. The number of days between photostimulation and sexual maturity were reduced in the 160-day treatment because a higher percentage of the pullets had already begun partitioning energy towards those organs involved in reproductive function. Indicative of changes happening in the body, was the improvement in uniformity of body weight within a flock as the age at photostimulation increased

(Robinson et al., 1996). Both Hocking (1996) and Robinson et al. (1996) have stated that the period before the onset of lay is critical. Therefore, for the onset of lay delaying photostimulation until flock uniformity is increased is beneficial.

Egg Parameters

One benefit of delaying photostimulation until pullets are older is that flock uniformity is improved and birds respond to photostimulation more quickly (Robinson et al., 1996). However what effect does delayed sexual maturity have on egg production, egg weight, fertility, and hatchability? In Leghorn pullets, a difference of 6 weeks in age at photostimulation had no effect on total egg production but the early-photostimulated birds produced more smaller eggs (Harrison et al., 1969). Turkeys photostimulated at 24 weeks of age had a higher incidence of multiple ovulations than poults photostimulated at 30 weeks of age (Hocking et al., 1988). Early-photostimulated turkeys had a lower peak egg production, which was explained by a lower number of LYF and a higher number of atretic follicles at 55 weeks of age (Hocking et al., 1988). In addition, a higher percentage of the early-photostimulated turkeys ceased laying as they got older. The effects of age at photostimulation are different for broiler breeder egg parameters. Yuan et al. (1994) found that age at photostimulation did not affect total egg production because the later-photostimulated pullets that achieved sexual maturity last had higher peak egg production and rate of lay from 28 to 35 weeks of age than early-photostimulated birds. Robinson et al. (1996) also found no differences in egg production. Likewise, mean egg weight and the number of settable eggs was not affected by delaying photostimulation (Yuan et al., 1994; Robinson et al., 1996). Fertility and hatchability were unaffected by age at photostimulation but the 140, 150, and 160-day treatments resulted in the production of more chicks per hen compared to 120 and 130-day treatments (Robinson et al., 1996).

Determining the appropriate age at which to photostimulate birds is that which results in a mature body size at an adult age. However with advancements in growth rate and breast muscle yield, broiler chickens can achieve a mature frame size (i.e. 2 kg body weight) by 42 days of age.

As such, the age at which sexual maturity occurs is changing. Eitan and Soller (1996) demonstrated that broiler breeders selected for a high body weight at sexual maturity are delayed coming into sexual maturation compared to birds that are selected for a low body weight. The difference in response is partly caused by a weaker photoperiodic drive in the heavy weight breeders (Eitan and Soller, 1996). Leeson et al. (1988) also noted that heavy weight birds have a curvilinear relationship between age at photostimulation and sexual maturity. Thus as genetic selection for increased body weight continues, photostimulating broiler breeders earlier will not advance the age at first oviposition, as some birds may be too young to respond to the light cue (Robinson et al., 1996). Young birds are still undergoing skeletal growth and have not diverted energy into fat deposition or ovary and oviduct development. Consequently, flock uniformity of body weight and rate of sexual maturity declines. This results in the production of smaller eggs (Harrison et al., 1969) and a lower rate of egg production (Yuan et al., 1994). Therefore, determining the appropriate age to photostimulate a broiler breeder flock depends on genetic factors, body weight, and age.

1.4 THE INCIDENCE OF PHOTOREFRACTORINESS IN POULTRY

Despite the beneficial effects of using artificial photoperiods to stimulate reproductive development, the importance of seasonal variation in day length should not be dismissed as it serves to time the onset and duration of the breeding season. Prolonging a fixed stimulatory photoperiod, will not maintain reproductive function. It will result in a lack of response to the given photoperiod, a condition known as photorefractoriness.

If photostimulated at 22 wk of age (assuming appropriate frame size), hens will begin laying eggs within 2 to 3 weeks. The rate of egg production will increase for 4 to 6 weeks until reaching a maximum level. Shortly after that, the rate of egg production declines and continues to do so until the production cycle is terminated. This pattern of egg production is similar for all strains of chicken however it is more pronounced in broiler than egg-type strains (Williams and Sharp, 1978a). That is, broiler breeders typically do not achieve as high a maximum level of egg production as commercial layers and the tendency is for egg production to fall rapidly after the peak is achieved. Hocking and McCormack (1995) demonstrated that the small follicles in broiler hens were more sensitive to gonadotropins than small follicles of egg layer hens. This increased sensitivity to LH resulted in more than one LYF hierarchy. The end result was the production of fewer settable eggs (Hocking and McCormack, 1995).

Sharp et al. (1992) demonstrated that the reduction in egg production that occurred as the hen aged was partially due to the development of photorefractoriness. The term photorefractoriness refers to a total lack of response to the long-day photoperiod. Photorefractoriness causes the reproductive system to become inactive thus terminating the breeding season (Nicholls et al., 1988). In nature, this process is related to appropriately timing the reproductive events in the hen's life. Little information is available on the controlling factors that regulate this condition, therefore, studies using mammals and different species of birds provide some insight into the chicken's photorefractory response.

Nicholls et al. (1988) wrote an extensive review on photorefractoriness in birds. Gonadal regression and anestrous characterize photorefractoriness. In most photosensitive bird species, this condition occurs when the day length is longer than the day length required for photostimulation. For example, on an 11 h photoperiod, male European starlings were able to exhibited testicular growth without the onset of photorefractoriness. On a 13 h photoperiod, the starlings came into sexual maturation quickly but gonadal regression ensued (Falk and Gwinner, 1988). Photorefractoriness can be maintained for long periods of time and as such can not be alleviated until the birds are exposed to a period of short days (Nicholls et al., 1988).

There are two different forms of photorefractoriness (Nicholls et al., 1988). The first, known as absolute photorefractoriness, is when the breeding season is terminated by prolonged exposure to long day lengths and photosensitivity is only regained by exposure to short day lengths. Species of birds that are absolutely photorefractory include the European starling, tree sparrow, the canary, the mallard and the grouse. The other form of photorefractoriness is when decreasing day lengths after the summer solstice terminate the breeding season. However a further increase in photoperiod may restore gonadal development and reproductive function.

These birds, which include the Japanese quail, are said to be relatively photorefractory (Nicholls et al., 1988). Follett (1988) suggested that the two forms of photorefractoriness were identical but that the degree to which photorefractoriness was expressed differred among species. For example, domesticated chickens, reared in a light-tight facility, most likely exhibit relative photorefractoriness as the laying cycle can be extended beyond natural duration. However as previously mentioned, egg production declines as the hen progresses through the laying cycle. This raises the question: "is the rate of decline in egg production a factor of increased age, relative photorefractoriness, or both?"

Cause of Photorefractoriness

Age Related Changes in the Hen. Williams and Sharp (1978a) noted that in both meat and egg layer stocks, the rate of egg production declines as hens age. This is attributed to fewer LYF (Williams and Sharp, 1978a) and a decreased rate of follicular recruitment into the LYF hierarchy on the ovaries of older birds (Bahr and Palmer, 1989). Another difference between young and old hens is that the interval between ovulations lengthens as the hen ages (Bahr and Palmer, 1989). Presumably the follicle needs more time to be ovulated because of a decreased follicular sensitivity to LH. When increased doses of LH were administered to the ovarian follicles of older hens, ovulation rate was increased (Mougdal and Razdan, 1985). Increased adenyl cyclase activity is an indicator of increased follicular maturation (Johnson et al., 1986). Old hens (53 to 63 weeks old) have lower LH-stimulated adenyl cyclase activity in the granulosa cells of the two largest follicles than young hens (28 to 38 weeks of age) (Johnson et al., 1986). A decreased sensitivity to LH in the F1 follicle of older hens would increase the time needed to elicit both the pre-ovulatory LH surge and ovulation thus causing the rate of egg production to decline (Johnson et al., 1986). However, chronologically, the 'old' hens used in these studies were little more than one year old. As chickens can live for up to 20 years (Romanoff and Romanoff, 1949), age itself is probably not the only contributing factor to the decrease in egg production and in LYF number in the ovary. In addition, the use of forced molting practices can increase egg production in older egg laying hens. As Sharp et al. (1992) suggested, the alteration in the sensitivity of the hypothalamus to LH may be a result of the development of photorefractoriness.

Alteration in the Sensitivity of the Hypothalamus. Williams and Sharp (1978b) noted that the pituitary's response to injections of GnRH and the ovarian response to injections of LH were not affected by the age of the hen. However, progesterone injection into old hens failed to stimulate a high LH response as in younger hens (Williams and Sharp, 1978b). This suggests that the changes occurring at the ovarian level were a result of a change in the sensitivity of either the hypothalamus or the pituitary to steroid hormone stimulation. Dawson et al. (1985) found that European starlings had no difference in hypothalamic GnRH concentration for the first 6 weeks after photostimulation compared to non-photostimulated starlings. However, the following 6 weeks were marked by a decrease in GnRH concentration as the birds became photorefractory. Similarly, the GnRH-I concentration in the median eminence of the hypothalamus was higher in egg-type hens that were laying (3.36 pmol/tissue) than in those that were not laying (2.13 pmol/tissue) (Sharp et al., 1990). A decrease in GnRH production would result in reduced amounts of GnRH released from the hypothalamus, decreasing the synthesis and release of gonadotropins from the anterior pituitary. Without adequate support from the higher components of the reproductive axis, the hen would cease laying. A similar pattern was uncovered in the domestic sheep, where it was found that GnRH pulse frequency decreased during anestrous (Goodman and Meyer, 1984). This implied that the mechanism involved in the photorefractory condition was directly influencing hypothalamic function.

Possible Factors Influencing the Hypothalamus

Neuronal Inputs. Although the mechanism of photorefractoriness is unknown, it is apparent that the reduction in reproductive function is linked to the hypothalamus, and possibly, is related to the same mechanism that is involved in photostimulation. In reviewing this topic, Sharp (1993) postulated that the changes in reproductive function might be caused by an inhibitory input to GnRH neurons. Long days transmit both positive (excitatory) and negative (inhibitory) signals into the hypothalamus. These inputs are either neuronal or hormonal and most likely originate outside the reproductive axis. For the first few weeks after photostimulation, the excitatory inputs are strong allowing for GnRH production and release. Meanwhile the inhibitory inputs develop gradually such that after prolonged exposure to long days, the inhibitory inputs dominate the excitatory inputs thereby terminating gonadal function. Transferring birds to short days results in the eventual withdrawal of the inhibitory inputs thus allowing the bird to regain photosensitivity to long day lengths. An immunocytochemical study done on European starlings found significantly more axonomic terminals and synaptic modifications during the photorefractory state than during other stages in the reproductive cycle (Parry and Goldsmith, 1993). This increase could be explained by an increase in inhibitory inputs causing a reduction in the secretion of GnRH (Parry and Goldsmith, 1993).

Goodman and Meyer (1984) suggested that GnRH secretion in the ewe is also controlled by inhibitory neurons. The inhibitory neuronal system is activated by short day lengths (as sheep are short-day breeders) resulting in a decline in tonic LH secretion leading to anestrus (Goodman and Meyer, 1984). In general, mammalian studies indicate that dopamine inhibits (Kuljis and Advis, 1989) while neuropeptide Y stimulates (Crowley and Kalra, 1987) GnRH release. Allen and Kalra (1986) demonstrated that administration of naloxone, an opioid antagonist, suppresses the inhibitory effects of endogenous opioid peptides on GnRH release in the rat. Evidence of a synapase between dopamine- and GnRH-containing neurons within the median eminence of the ewe lends further support to this theory (Kuljis and Advis, 1989).

Contijoch et al. (1992) found that hens also have a synaptic connection between dopamine-containing neurons and GnRH-containing terminals. There are also potential synaptic interactions with β-endorphin and neuropeptide Y (Contijoch et al., 1993a; 1993b). β-Endorphin is capable of blocking ovulation and suppressing LH concentrations *in vitro* (Sakurai et al., 1986). An opioid agonist, enkephalin, inhibits GnRH-I release from the medio-basal hypothalamus, whereas, administration of naloxone stimulates GnRH-I release in the cockerel (Stansfield and Cunningham, 1988). Lal et al. in 1990 found that naloxone did not stimulate GnRH-I or LH release in cockerels. However, ovulatory failure induced by feed withdrawal in Leghorn hens was associated with an increase in dopamine turnover and a decrease in GnRH release from the median eminence (Contijoch et al., 1992). As GnRH content decreased, serum concentrations of LH and progesterone also decreased (Contijoch et al., 1992). The possibility of synaptic interactions between opioid peptides and GnRH neurons requires further study and the regulation of the inhibitory and stimulatory inputs is uncertain. The possible involvement of thyroid hormones and prolactin in terminating estrous is discussed in the next section.

Thyroid Hormones and Prolactin. Changes in plasma thyroxine follow a diurnal pattern (Harvey et al., 1980) and plasma prolactin concentration increases in response to photostimulation (Sreekumar and Sharp, 1998). Both prolactin and thyroid hormones are involved in the regulation of the postnuptial molt, a characteristic of photorefractoriness (Nicholls et al., 1988). Dawson (1984) conducted a study on male and female European starlings that were exposed to various increases in photoperiod after being reared on 8 hours of light/day. Repeated blood samples were taken to assess thyroxine concentration and photorefractoriness was assessed at 2-week intervals by gonadal status through laparotomy. Birds that were photostimulated with either 13 hours or 18 hours of light/day had high levels of plasma thyroxine (5.2 and 11.9 nmol/L, respectively). These birds subsequently underwent a molt, 12 weeks after photostimulation in the 13 hours of light/day treatment and 9 weeks after photostimulation in the 18 hours of light/day treatment. Alternatively, starlings that were held on 8 hours of light/day or photostimulated with 11 hours of light/day did not exhibit any change in their plasma thyroxine levels (less than 5 nmol/L for both treatments) and they did not molt (Dawson, 1984). Starlings on the 13 and 18 hour day lengths went photorefractory with the concentration of prolactin increasing before photorefractoriness occurred (18.9 to 21.2 μg/L compared to 1.9 μg/L before photostimulation; Dawson and Goldsmith, 1983). Starlings on the 8 and 11 hour day lengths did not become photorefractory and prolactin levels remained low (Dawson and Goldsmith, 1983).

Thyroid hormones were thought to act on the hypothalamus inhibiting the release of GnRH and causing photorefractoriness to occur (Dawson, 1984). Therefore, the effects of thyroidectomy were studied. Removal of the thyroid glands in starlings held on a short photoperiod and then transferred to a long photoperiod resulted in sexual maturation but the occurrence of photorefractoriness was abolished, whereas thyroid-intact starlings had become photorefractory within 12 weeks (Dawson et al., 1985). Thyroidectomized starlings also have low circulating prolactin concentrations suggesting that prolactin was also related to photorefractoriness (Goldsmith and Nicholls, 1984a; 1984b; Dawson et al., 1985). However, recent studies would indicate that the increase in prolactin secretion that occurs at the end of the breeding season is necessary for the process of gonadal regression but is not necessary for the development of photorefractoriness (Dawson and Sharp, 1998; Sreekumar and Sharp, 1998). Immunization against vasoactive intestinal polypeptide, the prolactin releasing hormone, did not prevent photorefractoriness (Dawson and Sharp, 1998). Although prolactin is not the direct cause of photorefractoriness some studies are focused on prolactin receptor gene expression in the hypothalamus and its relationship to the reproductive state of the bird (Ohkubo et al., 1998a; b).

Thyroid hormones are also not responsible for inducing photorefractoriness, despite the convincing evidence obtained using thyroidectomized starlings. Bentley et al. (1997) thyroidectomized starlings and then administered different dosages of thyroxine. Treating the starlings with thyroxine reversed the effects of thyroidectomy and photorefractoriness ensued (Bentley et al., 1997). However, photorefractoriness occurred when concentrations of thyroxine were lower than levels found in intact starlings on short-days (0.045 to 0.18 mg/L). Therefore, Bentley et al. (1997) concluded that thyroxine did not drive the photorefractory state, rather it acted as a permissive factor, allowing photorefractoriness to occur.

In domestic sheep, the inhibitory inputs are controlled by the estradiol negative feedback system (Legan and Karsch, 1979). Moenter et al. (1991) speculated that an increase in thyroid hormone concentration influenced the inhibitory inputs heightening the responsiveness to the negative feedback effects of estradiol. The neuronal inputs to the GnRH system can change seasonally, with a substantial decrease in GnRH synaptic density during anestrus as compared to the breeding season in the ewe (Xiong et al., 1997). Thrun et al. (1997) speculated that once the thyroid hormone-dependent synaptic inputs are in place and suppression of breeding has occurred, thyroid hormones were no longer needed to sustain these inputs. A similar mechanism may exist in avian species.

Regulation by Estrogen. The estradiol negative feedback system has been clearly shown to regulate reproductive cyclicity in the sheep. Seasonal variation in the number of GnRH neurons could be controlled by changes in photoperiod or in an endogenous circannual rhythm (Xiong et al., 1997). In the cockerel, testosterone serves to exert negative feedback on the hypothalamus, depressing concentrations of GnRH and subsequently LH (Stansfield and Cunningham, 1988). As the male approaches puberty, the hypothalamus is believed to become less sensitive to this negative feedback mechanism so that eventually GnRH is released in sufficient quantities and sexual maturation can occur. Stansfield and Cunningham (1988) found that testosterone acted on the hypothalamus via opioid peptides, implying that the negative feedback mechanism that controls GnRH synthesis and release in the ewe may also apply to chickens.

Methods of Avoiding Photorefractoriness in Chickens

The site at which photorefractoriness occurs is evidently at the hypothalamic level, as the anterior pituitary and the gonads are always responsive to hormonal stimulation regardless of the reproductive state of the bird (Dawson et al., 1985). As the hypothalamo-pituitary-gonadal axis is activated by a stimulatory photoperiod, it is possible that the photorefractory condition is mediated by the photoperiodic response of the bird. Based on the evidence collected from chickens and other species of birds, several different proposals on preventing photorefractoriness have emerged.

Determination of the Critical Day Length. A photoperiodic response curve represents the response of LH to various stimulatory photoperiods. Based on this curve the minimum day length required to stimulate a reproductive level of LH can be determined. This is known as the 'critical day length'. Increasing day length above the critical value stimulates higher concentrations of LH until a maximum concentration is reached. The photoperiod that induces this maximal level of LH is known as the 'saturation day length'. Beyond the saturation day length, any further increase in photoperiod has no effect on LH secretion (Sharp, 1984). Dunn and Sharp (1990) determined the photoperiodic response curves for both dwarf breeder and egg-type hens. Birds were subjected to different photostimulatory day lengths at 8 weeks of age and the concentration of plasma LH was measured. It was found that stimulatory levels of LH occurred at 10.5 hours of light/day in the dwarf strain and between 10.5 and 12.75 hours of light/day in the egg laying strain. These were the critical day lengths for the two strains respectively. Likewise, Dunn and Sharp (1990) noted that photoperiods above 12.75 hours for dwarf birds and 15.25 hours for egg-type birds did not result in any further increase in LH concentration. This was the saturation day length as LH concentrations were maximized. These data suggest that any photoperiod greater than the saturation day length will not improve the photoperiodic response in the bird as LH concentrations are already at maximal levels.

Siopes (1994) noted that the critical day length required to induce reproductive function varied seasonally in turkeys and was lower than the critical day length required for optimal egg production. The photoperiod for optimal egg production was equivalent to the saturation day length. During the summer, the critical day length for inducing egg production was 11 hours of light/day and for optimal egg production was 16 hours of light/day. During the winter, the critical day lengths for these responses were lower, being 10.5 hours of light/day and 11.5 hours of light/day for inducing egg production and optimal egg production, respectively (Siopes, 1994). In winter, the critical day length for photorefractoriness was 12 to 12.5 hours of light/day, higher than that for required egg production (Siopes, 1994). This suggests that photoperiods with day lengths longer than the critical day length for optimal egg production may drive the bird to a photorefractory state. However, Siopes (1994) found that when photoperiods below the critical day length for photorefractoriness were applied, the number of eggs was not different from when photoperiods above 12.5 hours of light/day were used. Morris et al. (1995) suggested that the photoperiods used in commercial laying barns (i.e. 15 to 17 hours of light/day) are higher than needed for full reproductive function. Various lighting regimes were employed to test the hypothesis that avoiding an increase in photoperiod beyond the saturation day length would prevent the onset of photorefractoriness (Morris et al., 1995). There were marginal differences in the overall rate of lay among hens given 11 versus 15 hours of light/day, therefore Morris et al. (1995) concluded that photorefractoriness does not result from using a long photoperiod in the first year of lay, however, photoperiods above 15 hours of light/day were not evaluated.

Increasing the Photoperiod After Photostimulation. Nicholls et al. (1988) suggested that the mechanism that allowed for absolute photorefractoriness was probably established soon after photostimulation had occurred, therefore, changes in day length that occurred after sexual maturity would be ineffective. This situation was applicable to turkeys. However, the mechanism for relative photorefractoriness was different, as providing a further increase in photoperiod during lay re-stimulated egg production, thereby preventing the onset of photorefractoriness. This further increase in photoperiod was believed to increase the GnRH output from the hypothalamus by enhancing the stimulatory inputs (Sharp, 1993). In the European starling, changes in photoperiod after the bird has reached sexual maturation are still able to affect the development of photorefractoriness (Falk and Gwinner, 1988). Starlings photostimulated with a 13 hour photoperiod typically achieved photorefractoriness while starlings on a 11 hour photoperiod did not. When birds were given 13 hours of light/day initially and then 11 hours of light/day, gonadal growth continued to occur but photorefractoriness did not develop (Falk and Gwinner, 1988). Sharp et al. (1992) found that when dwarf breeders were given an increase in day length from 14 to 20 hours of light/day at 28 weeks of age, egg production was higher than for hens that were maintained on 14 hours of light/day. This coincided with an increase in the plasma concentration of LH (Sharp et al., 1992). Similarly, Marr et al. (1962) found that egg layers given an additional 9 hours of light/day at 30 weeks of age had a higher overall egg production (67.7%) than birds that were not given any additional light after photostimulation (61.7 to 64.5%).

As chickens are believed to be capable of relative photorefractoriness, it is possible that the decline in egg production is the result of an inhibition on the GnRH neurons caused by the negative feedback effects of estrogen and other androgens. However, there are other factors that contribute to poor egg production such as genetic selection for growth rate, stress, and age. In a feed restricted broiler breeder it is most likely that all of the above factors play a role in governing reproductive status. The effect of different levels of dietary crude protein on the reproductive performance of hens is discussed in the next section.

1.5 PROTEIN INTAKE EFFECTS ON REPRODUCTIVE PARAMETERS

In commercial layer operations, *ad libitum* access to feed ensures that the bird's nutritional needs are met (for example, requirements for dietary protein). For broiler breeder production, feed restriction must be practiced because heavy selection for growth rate leads to obesity in *ad libitum* fed broiler breeders (Siegel and Dunnington, 1985). Unfortunately, a definition of the optimal level of crude protein intake has not been determined for broiler breeders. The NRC (1994) does not specify a dietary crude protein level because chickens do not require an absolute level of protein in their diet. Rather, chickens need essential amino acids and amino nitrogen for the synthesis of non-essential amino acids, therefore some level of crude protein must be provided in the diet (NRC, 1994). Of critical importance is understanding how protein requirements change depending on age and reproductive status. The transition from pullet to hen is one stage where protein requirements may change. At this stage, skeletal and muscle growth slows down as fat deposition and growth of reproductive organs increases (Robinson et al., 1996). Therefore this period is important as a diet with a low level of protein will lead to sub-optimal reproductive performance whereas a high amount of protein may lead to problems with excessive fat deposition and increased body weight. The effect of different dietary crude protein levels during the pullet to layer and laying periods is discussed below.

Amino Acids versus Crude Protein Intake

As chickens do not require a specific level of crude protein in their diet several studies have focussed, rather, on determining the specific essential amino acid requirement for optimal reproductive performance. Methionine, lysine, and tryptophan are the first three limiting amino acids for broiler breeder hens (Harms, 1992). It has been shown that decreasing the level of lysine and methionine often results in poorer egg production (Pearson and Herron, 1981; Bowmaker and Gous, 1991; Harms, 1992; Harms and Russell, 1995). Harms (1992) found that to produce 45.7 g of egg output per day a broiler breeder hen requires 814 mg of lysine and 429 mg of methionine per day. This is somewhat higher than Bowmaker and Gous' (1991) estimate of 723 and 321 mg of lysine and methionine, respectively for the same egg output. In 1995, Harms and Russell stated that 845 mg of lysine per day was needed for optimal levels of egg production, egg mass, and egg content however only a 6 week test period was used beginning at 34 weeks of age, which was past the age of peak egg production. All three estimates of the lysine requirement differed from the NRC (1994) recommendation of 765 mg per day.

The above studies illustrate the difficulty in determining the correct amino acid composition of the diet; however, there are also other complications with formulating diets this way. For one, most of the requirements for amino acid levels have been determined based on *ad libitum* fed egg-type hens. The requirements for broiler breeders are different because they are a heavier bird, therefore they will have a higher maintenance requirement, and they are feed restricted (Bornstein et al., 1979). Even work that has been done on broiler breeders is difficult to interpret because requirements are usually determined on individually caged birds. Flock estimates based on consumption by caged breeders are usually lower than what is actually needed because of individual variability (Bowmaker and Gous, 1991). Another problem is that the amino acid requirements for optimal reproductive performance may differ depending on the parameter measured. For instance, Harms and Ivey (1992) found that 806 mg of lysine was needed for maximum egg production but 819 mg was needed for maximum egg mass. Lastly, if only specific amino acids are increased, while others are left at minimum levels, this may lead to imbalances in amino acid intake. In this case, the first amino acid that is in insufficient supply will limit the utilization of the other amino acids even if they are present in excess amounts. Furthermore, the appropriate ratio of essential to non-essential amino acids is unknown (Lopez and Leeson, 1994). Thus, the other option, rather than changing specific amino acid levels, is to change the level of crude protein intake focussing on altering the amino acid levels proportionately.

Influence of Dietary Protein on Egg Weight

Increasing early egg size is an important issue to Canadian hatching egg producers because eggs that are too small often result in the production of low body weight chicks. The use of additional protein in the diet to increase egg weight has been investigated but results have been conflicting. Hawes and Kling (1993) found that a higher level of crude protein (17 compared to 13%) fed to brown egg layers improved egg size. Cave (1984) and Brake et al. (1985) found that there was no effect of additional protein in the pre-breeder diet on egg weight. Waldroup et al. (1976) found that if the protein level in the diet increased from 14.5 to 20 g/day, egg weight also increased. However, when 22 g/day was fed, there was no additional improvement in egg weight. Waldroup et al. (1976) concluded that at 20 g of protein per day, equivalent to 13.7% CP, the hens amino acid requirement for optimal egg size were met. However Spratt and Leeson (1987) noted that egg weight increased when 16.7% CP was provided in the diet (versus 12.7% CP). The breeders fed the high protein diet were heavier, which likely contributed to increased egg weight (Spratt and Leeson, 1987). McDaniel et al. (1981) demonstrated that body weight was positively correlated with egg weight. Summers and Leeson (1983) reported no difference in early egg size of egg-layers when fed either 17 or 22% CP from 20 to 32 weeks of age. Body weight of the young layer affected egg size more than dietary protein or fat (Summers and Leeson, 1983). Although early egg size was not altered by additional protein, for the first 3 weeks of laying, egg size remained high thereafter in the hens fed the high protein diet. In another study, in response to increase dietary protein, differences in egg weight in broiler breeders were only found at 60 wk of age (Lopez and Leeson, 1995). In protein deficient diets, the proportion of yolk and shell increased while albumen decreased (Fisher, 1969). This was largely a reflection of decreased egg weight (Fisher, 1969). While additional protein in the diet beyond a certain level does not seem to improve egg weight, a diet that is deficient in protein will decrease egg size. Compared to higher levels of crude protein, 12% CP resulted in the smallest egg size (Butts and Cunningham, 1972). This treatment may have been deficient in the essential amino acids or the amino nitrogen required for egg formation as the concentrations of albumen and whole egg protein increased as dietary protein was increased above 12% CP (Butts and Cunningham, 1972).

Influence of Dietary Protein on Egg Production

In 1984, the NRC stated that a minimum of 22 g of protein/day should be fed to breeders. In 1994, that value was decreased to 19.5 g/day (NRC, 1994). In terms of reproductive performance, birds given 19.4 g of protein/day performed as well as birds receiving more protein (i.e. 24.6 g of protein/day; Pearson and Herron, 1981). Spratt and Leeson (1987) agreed that 19 g of protein/day (12.7% CP) could support normal reproductive performance in broiler breeders. Harms and Russell (1995) estimated that the crude protein requirement was even lower being 18.1 g of protein/day (10.95% CP). At this level, the requirements for egg production, egg mass, and egg content were satisfied (Harms and Russell, 1995). It would appear then, that there is little benefit to increasing the crude protein content of the diet. However both Cave (1984) and Brake et al. (1985) found that egg production increased in response to a high protein diet. A difference of 189 g of protein per bird during the pre-breeder period resulted in 9.6 more eggs in the Cave (1984) trial and 140 g of protein per bird produced 5.7 more eggs in the Brake et al. (1985) trial. In both experiments the differences in egg number occurred after peak production. Likewise, in another study, increased protein intake (23 compared to 16% CP) from 18 to 25 weeks of age increased egg production from 28 to 36 weeks of age (Lilburn and Myers-Miller, 1990). Although the effects of added protein during the pre-breeder period were somewhat delayed, Brake et al. (1985) demonstrated that nutrient intake between the pullet to hen transition period could affect future reproductive performance.

Influence of Dietary Protein on Carcass Characteristics

There are few studies that report the effect of dietary protein on the reproductive performance of breeders. There are even fewer studies that describe the effect of protein on carcass components. As already mentioned, high levels of protein during lay has little effect on body weight (Summers and Leeson, 1983; Cave, 1984; Spratt and Leeson, 1987; Summers and

Leeson, 1993). Low levels of dietary protein or lysine during the growing phase lowers the body weight of pullets; however, the only carryover effect on the laying period is a delay in sexual maturity (Singsen et al., 1965; Waldroup et al., 1966; Harms et al., 1968; Luther et al., 1976). A high protein diet (23% CP) fed during rearing resulted in an increase in breast muscle weight and a decrease in abdominal fat pad weight as compared to a 16% CP diet at 13 or 18 weeks of age (Lilburn and Myers-Miller, 1990). By 25 weeks of age, there was no effect of rearing period protein level or pre-lay period protein level on carcass characteristics (Lilburn and Myers-Miller, 1990). Pearson and Herron (1981) found no effect of protein intake on carcass protein at 64 weeks of age. Spratt and Leeson (1987) also found no differences in carcass protein but did note that a low protein intake increased carcass fat content (52.4%, dry matter) compared to the high protein intake (48.9%, dry matter). Unfortunately, there is not enough evidence available to draw any substantial conclusions of protein on carcass composition.

While these previous studies have reported beneficial effects of increased dietary protein on egg production, there is not enough evidence to conclude that current high breast yield birds would respond similarly as did broiler breeders 10 to 15 years ago. It is possible that there is a limit to the effect of increasing dietary CP on egg weight and egg production (Fisher, 1998). Pearson and Herron (1981) found that diets containing more than 63 g of protein per Mcal apparent metabolizable energy (AME) reduced egg production and hatchability in broiler breeders. Dietary protein beyond this upper limit may actually increase body weight as broiler breeders today have been selected for rapid growth and increased breast muscle mass. Therefore, detailed research in this area is still required.

1.6 DESCRIPTION OF EXPERIMENTS

Objective

The objective of this program was to determine the effects of different management techniques on the reproductive performance and carcass characteristics of female broiler breeders. Specifically, the level of crude protein in the diet, the age at photostimulation, and the application of a further increase in day length after peak production were examined.

Experiments

1. **Objective:** To determine the effect of additional dietary protein during the pre-lay and early-lay period on broiler breeder performance.

   Description: Broiler breeder pullets were given 14, 16, or 18% CP in their diet from 20 to 29 weeks of age. The age at sexual maturity, egg weight, and egg production were assessed. Carcass composition was determined at 29 weeks of age to compare in carcass protein, fat, moisture, and ash resulting from the three diets.

2. **Objective:** To study the effect of delaying the age at photostimulation on age at sexual maturity, early egg size, sequence length, and other reproductive parameters.

   Description: Three different strains of broiler breeder females were photostimulated at either 20 or 23 weeks of age. Data on individual egg production were collected throughout the trial to 54 weeks of age.

3. **Objective:** To determine if an increase in day length after peak egg production re-stimulates ovulation rate and egg production.

   Description: Two strains of broiler breeders were either held on the initial photostimulatory day length of 14 hours of light/day or were subjected to an additional 30 minutes of light/day beginning at 33 weeks of age (to 18 hours of light/day by 40 weeks of age). Birds were processed at various ages to determine strain differences in carcass characteristics and if the additional hours of light affected ovarian parameters.

1.7 REFERENCES

Ali, A., and K. M. Cheng, 1985. Early egg production in genetically blind (rc/rc) chickens in comparison with sighted (Rc^+/rc) controls. Poultry Sci. 64: 789-794.

Allen, L. G., and S. P. Kalra, 1986. Evidence that a decrease in opioid tone may evoke preovulatory luteinizing hormone release in the rat. Endocrinology 118:2375-2381.

Armstrong, D. G., 1985. Changes in aromatase activity in small ovarian follicles of the domestic fowl (*Gallus domesticus*) during growth and atresia. J. Endocrinol. 105: 297-301.

Bahr, J. M., and A. L. Johnson, 1984. Regulation of the follicular hierarchy and ovulation. J. Exp. Zool. 232: 495-500.

Bahr, J. M., and S. S. Palmer, 1989. The influence of aging on ovarian function. Crit. Rev. Poult. Bio. 2:103-110.

Bahr, J. M., S. -C., Wang, M. Y. Huang, and F. O. Calvo, 1983. Steroid concentrations in isolated theca and granulosa layers of preovulatory follicles during the ovulatory cycle of the domestic hen. Biol. Reprod. 29: 326-334.

Benoit. J., 1964. The role of the eye and of the hypothalamus in the photostimulation of the gonads in the duck. Ann. N.Y. Acad. Sci. 117: 204-216.

Bentley, G. E., A. R. Goldsmith, A. Dawson, and L. M. Glennie, R. T. Talbot, and P. J. Sharp, 1997. Photorefractoriness in European starlings (*Sturnus vulgaris*) is not dependent upon the long-day induced rise in plasma thyroxine. Gen. Comp. Endocrinol. 107:428-438.

Bernard, M., J. Guerlotte, P. Greve, A. Grechez-Cassiau, P. M. Iuvone, M. Zatz, N. W. Chong, D. C. Klein, and P. Voisin, 1999. Melatonin synthesis pathway: circadian regulation of the genes encoding the key enzymes in the chicken pineal gland and retina. Reprod. Nutr. Dev. 39: 325-334.

Bernard, M., P. M. Iuvone, V. M. Cassone, P. H. Roseboom, S. L. Coon, and D. C. Klein, 1997. Avian melatonin synthesis: photic and circadian regulation of sertonin *N*-acetyltransferase mRNA in the chicken pineal gland and retina. J. Neurochem. 68: 213-224.

Binkley, S., M. Hryschchyshyn, and K. Reilly, 1979. *N*-acetyltransferase activity responds to environmental lighting in the eye as well as the pineal gland. Nature 281: 479-481.

Bonney, R. C., F. J. Cunningham, and B. J. A. Furr, 1974. Effect of synthetic luteinizing hormone releasing hormone on plasma luteinizing hormone in the female domestic fowl, *Gallus domesticus*. J. Endocrinol. 63: 539-547.

Bonney, R. C., and F. J. Cunningham, 1977. The sensitizing effect of oestradiol on the response of the anterior pituitary gland of the domestic fowl to luteinizing hormone releasing hormone *in vitro* and *in vivo*. J. Endocrinol. 72: 16P.

Bornstein, S., S. Hurwitz, and Y. Lev, 1979. The amino acid and energy requirements of broiler breeder hens. Poultry Sci. 58:104-116.

Bowmaker, J. E., and R. M. Gous, 1991. The response of broiler breeder hens to dietary lysine and methionine. Br. Poult. Sci. 32:1069-1088.

Brake, J., J. D. Garlich, and E. D. Peebles, 1985. Effect of protein and energy intake by broiler breeders during the prebreeder transition period on subsequent reproductive performance. Poultry Sci. 64:2335-2340.

Brody, T. B., P. B. Siegel, and J. A. Cherry, 1984. Age, body weight and body composition requirements for the onet of sexual maturity of dwarf and normal chickens. Br. Poult. Sci. 25: 245-252.

Bullock, R. W., and A. V. Nalbandov, 1967. Hormonal control of the hen's ovulatory cycle. J. Endocrinol. 38: 407-415.

Butts, J. N., and F. E. Cunningham, 1972. Effect of dietary protein on selected properties of the egg. Poultry Sci. 51:1726-1734.

Cave, N. A. G., 1984. Effect of a high-protein diet fed prior to the onset of lay on performance of broiler breeder pullets. Poultry Sci. 63:1823-1827.

Contijoch, A. M., C. Gonzalez, H. N. Singh, S. Malamed, S. Troncoso, and J. P. Advis, 1992. Dopaminergic regulation of luteinizing hormone-releasing hormone release at the median eminence level:immunocytochemical and physiological evidence in hens. Neuroendocrinology 55:290-300.

Contijoch, A. M., S. Malamed, J. K. McDonald, and J. P. Advis, 1993a. Neuropeptide Y regulation of LHRH release in the median eminence:immunocytochemical and physiological evidence in hens. Neuroendocrinology 57:135-145.

Contijoch, A. M., S. Malamed, D. K. Sarkar, and J. P. Advis, 1993b. β-Endorphin regulation of LHRH release at the median eminence level:immunocytochemical and physiological evidence in hens. Neuroendocrinology 57:365-373.

Crowley, W. R., and S. P. Kalra, 1987. Neuropeptide Y stimulates the release of luteinizing hormone-releasing hormone from medial basal hypothalamus *in vitro*:modulation by ovarian hormones. Neuroendocrinology 46:97-103.

Dawson, A., 1984. Changes in plasma thyroxine concentrations in male and female starlings (*Sturnus vulgaris*) durinng a photo-induced gonadal cycle. Gen. Comp. Endocrinol. 56:193-197.

Dawson, A., B. K. Follett, A. R. Goldsmith, and T. J. Nicholls, 1985. Hypothalamic gonadotropin-releasing hormone and pituitary and plasma FSH and prolactin during photostimulation and photorefractoriness in intact and thyroidectomized starlings (*Sturnus vulgaris*). J. Endocrinol. 105:71-77.

Dawson, A., and A. R. Goldsmith, 1983. Plasma prolactin and gonadotropins during gonadal development and the onset of photorefractoriness in male and female starlings (*Sturnus vulgaris*) on artificial photoperiods. J. Endocrinol. 97:253-260.

Dawson, A., and P. J. Sharp, 1998. The role of prolactin in the development of reproductive photorefractoriness and post-nuptial molt in the European starling (*Sturnus vulgaris*). Endocrinology 139:485-490.

Dunn, I. C. and P. J. Sharp, 1990. Photoperiodic requirements for LH release in juvenile broiler and egg-laying strains of domestic chickens fed *ad libitum* or restricted diets. J. Reprod. Fertil. 90:329-335.

Dunn, I. C., and P. J. Sharp, 1999. Photo-induction of hypothalamic gonadotrophin-releasing hormone-I mRNA in the domestic chicken: a role for oestrogen? J. Neuroendocrinology 11: 371-375.

Eitan, Y., and M. Soller, 1996. Selection for high and low threshold body weight at first egg in broiler strain females. 6. Threshold body weight for onset of photosensitivity in females of the selection lines. Poultry Sci. 75:459-463.

Ernst, R. A., J. R. Millam, and F. B. Mather, 1987. Review of life-history lighting programs for commercial laying fowls. World's Poultry Sci. 43:45-55.

Etches, R. J., and F. J. Cunningham, 1975. The role of the pre-ovulatory release of progestone in the chicken. J. Endocrinol. 64: 47P-48P.

Etches, R. J., and F. J. Cunningham, 1976. The interrelationship between progesterone and luteinzing hormone during the ovulation cycle of the hen (*Gallus domesticus*). J. Endocrinol. 71:51-58.

Falk, H., and E. Gwinner, 1988. Timing of photorefractoriness in the European starling: significance of photoperiod early and late in the reproductive cycle. Biol. Reprod. 39:1004-1008.

Farner, D., 1964. The photoperiodic control of reproductive cycles in birds. Am. Scientist 52:137-156.

Fisher, C., 1969. The effects of a protein deficiency on egg composition. Br. Poult. Sci. 10:149-154.

Fisher, C. 1998. Amino acid requirements of broiler breeders. Poultry Sci. 77:124-133.

Follett, B. K., 1988. Refractoriness in quail leads to a reduction in the photoperiodic drive on LH secretion. J. Endocrinol. 116:363-366.

Foster, D. L., F. J. Karsch, D. H. Olster, K. D. Ryan, and S. M. Yellon, 1986. Determinants of puberty in a seasonal breeder. Rec. Prog. Horm. Res. 42:331-384.

Fraps, R. M., 1954. Neural basis of diurnal periodicity in release of ovulation-inducing hormone in fowl. Proc. Natl. Acad. Sci. 40:348-356.

Fraps, R. M., 1961. Ovulation in the domestic fowl. Pages 133-162 *in*: Control of ovulation. C. A. Villee, ed. Pergamon Press, New York, NY.

Furr, B. J. A., R. C. Bonney, R. J. England, and F. J. Cunningham, 1973. Luteinizing hormone and progesterone in the peripheral blood during the ovulatory cycle of the hen *Gallus domesticus*. J. Endocrinol. 57: 159-169.

Gilbert, A. B., 1971. The ovary. Pages 1163-1202 *in:* Physiology and Biochemistry of the Domestic Fowl. D. J. Bell and B. M. Freeman, ed. Academic Press Inc., London, England.

Gilbert, A. B., M. M. Perry, D. Waddington, and M. A. Hardie, 1983. Role of atresia in establishing the follicular hierarchy in the ovary of the domestic hen (*Gallus domesticus*). J. Reprod. Fert. 69: 221-227.

Gilbert, A. B., and Wells, 1984. Structure and function of the ovary. Pages 15-27 *in:* Reproductive Biology of Poultry. F. J. Cunningham, P. E. Lake, and D. Hewitt, ed. British Poultry Science Ltd., Longman Group, Harlow, England.

Goldsmith, A. R., and T. J. Nicholls, 1984a. Prolactin is associated with the development of photorefractoriness in intact, castrated, and testosterone-implanted starlings. Gen. Comp. Endocrinol. 54:247-255.

Goldsmith, A. R., and T. J. Nicholls, 1984b. Thyroidectomy prevents the development of photorefractoriness and the associated rise in plasma prolactin in starlings. Gen. Comp. Endocrinol. 54:256-263.

Goodman, R. L., and S. L. Meyer, 1984. Effects of pentobarbital anesthesia on tonic luteinizing hormone secretion in the ewe: evidence for active inhibition of luteinizing hormone in anestrus. Biol. Reprod. 30:374-381.

Hamm, H. E., and M. Menaker, 1980. Retinal rhythms in chicks: circadian variation in melatonin and serotonin N-acetyltransferase activity. Proc. Natl. Acad. Sci. 77:4998-5002.

Hammond, R. W., H. Todd, and F. Hertelendy, 1980. Effects of mammalian gonadoptropins on progesterone release and cyclic nucleotide production by isolated avian granulosa cells. Gen. Comp. Endocrinol. 41: 467-476.

Harms, R. H., 1992. A determination of the order of limitation of amino acids in a broiler breeder diet. J. Appl. Poultry Res. 1:410-414.

Harms, R. H., B. L. Damron, and H. R. Wilson, 1968. Performance of broiler breeder pullets as influenced by composition of grower and layer diets. Br. Poult. Sci. 9:359-366.

Harms, R. H., and F. J. Ivey, 1992. An evaluation of the protein and lysine requirement for broiler breeder hens. J. Appl. Poultry Res. 1:308-314.

Harms, R. H., and G. B. Russell, 1995. A re-evaluation of the protein and lysine requirement for broiler breeder hens. Poultry Sci. 74:581-585.

Harrison, P. C., W. C. Becker, 1969. Extra retinal photocontrol of oviposition in pinealectomized domestic fowl. Proc. Soc. Exp. Biol. Med. 132: 161-164.

Harrison, P. C., G. Schumaier, and J. McGinnis, 1969. Reproductive development and response of white leghorn pullets subjected to increasing day-lengths at different ages. Poultry Sci. 48: 1021-1026.

Harvey, S., T. F. Davidson, H. Klandorf, and J. G. Philips, 1980. Diurnal changes in the plasma concentrations of thyroxine and triiodothyronine and their binding to plasma proteins in the domestic duck (*Anas platyrhynchos*). Gen. Comp. Endocrinol. 42:500-504.

Hawes, R. O., and L. J. Kling, 1993. The efficacy of using prelay and early-lay rations for brown-egg pullets. Poultry Sci. 72:1641-1649.

Hocking, P. M., 1996. Role of body weight and food intake after photostimulation on ovarian function at first egg in broiler breeder females. Br. Poultry Sci. 37:841-851.

Hocking, P. M., A. B. Gilbert, C. C. Whitehead, and M. A. Walker, 1988. Effects of age and of early lighting on ovarian function in breeding turkeys. Br. Poultry Sci. 29:223-229.

Hocking, P. M., and H. A. McCormack, 1995. Differential sensitivity of ovarian follicles to gonadotrophin stimulation in broiler and layer lines of domestic fowl. J. Reprod. Fert. 105:49-55.

Homma, K., L. Z., McFarland, and W. O. Wilson, 1967. Response of the reproductive organs of the Japanese quail to pinealectomy and melatonin injections. Poultry Sci. 46:314-319.

Homma, K., and M. Ohta, and Y. Sakakibara, 1980. Surface and deep photoreceptors in photoperiodism in birds. Pages 149-156 *in:* Biological Rhythms in Birds: Neural and Endocrine Aspects. Y. Tanabe, K. Tanaka, and T. Ookawa, ed. Japan Scientific Societies Press, Tokyo/Springer-Verlag, Berlin.

Huang, E. S., K. J. Kao, and A. V. Nalbandov, 1979. Synthesis of sex steroids by cellular components of chicken follicles. Biol. Reprod. 20: 454-461.

Iuvone, P. M., 1990. Development of melatonin synthesis is chicken retina: regulation of serotonin *N*-acetyltransferase activity by light, circadian oscillators, and cyclic AMP. J. Neurochem. 54:1562-1568.

Johnson, P. A., R. W. Dickerman, and J. M. Bahr, 1986. Decreased granulosa cell luteinizing hormone sensitivity and altered thecal estradiol concentration in the aged hen, *Gallus domesticus*. Biol. Reprod. 35:641-646.

Johnson, A. L., P. A. Johnson, and A. van Tienhoven, 1985. Evidence for a positive feedback interaction between progesterone and luteinizing hormone in the induction of ovulation in the hen, *Gallus domesticus*. Gen. Comp. Endocrinol. 58: 478-485.

Katanbaf, M. N., E. A. Dunnington, and P. B. Siegel, 1989. Restricted feeding early and late-feathering chickens. 2. Reproductive responses. Poultry Sci. 68:352-358.

Kawashima, M., M. Kamiyoshi, and K. Tanaka, 1979. Cytoplasmic progesterone receptor concentrations in the hen hypothalamus and pituitary: difference between laying and nonlaying hens and changes during the ovulatory cycle. Biol. Reprod. 20: 581-585.

Kawashima, M., M. Kamiyoshi, and K. Tanaka, 1993. Estrogen receptor binding in the hen hypothalamus and pituitary during the ovulatory cycle. Poultry Sci. 72: 839-847.

King, D. F., 1961. Effects of increasing, decreasing, and constant lighting treatments on growing pullets. Poultry Sci. 40: 479-487.

King, D. F., 1962. Egg production of chickens raised and kept in darkness. Poultry Sci. 41:1499-1503.

King, J. D., R. P. Millar, 1982. Structure of chicken hypothalamic luteinizing hormone-releasing hormone-II. Isolation and characterization. J. Biol. Chem. 257: 10729-10732.

Kuenzel, W. J., 1993. The search for deep encephalic photoreceptors within the avian brain, using gonadal development as a primary indicator. Poultry Sci. 72: 959-967.

Kuljis, R. O., and J. P. Advis, 1989. Immunocytochemical and physiological evidence of a synapse between dopamine- and luteinizing hormone releasing hormone-containing neurons in the ewe median eminence. Endocrinology 124:1579-1581.

Lal, P., P. J. Sharp, I. C. Dunn, and R. T. Talbot, 1990. Absence of an effect of naloxone, an opioid antagonist, on luteinizing hormone release *in vivo* and luteinizing hormone-releasing hormone I release *in vitro* in intact, castrated, and food restricted cockerels. Gen. Comp. Endocrinol. 77:239-245.

Leeson, S., R. J. Etches, and J. D. Summers, 1988. Development of Leghorn pullets subjected to early light stimulation. Can. J. Anim. Sci. 68:1267-1275.

Leeson, S., and J. D. Summers, 1983. Consequence of increased feed allowance for growing broiler breeder pullets as a means of stimulating early maturity. Poultry Sci. 62:6-11.

Legan, S. J., and F. J. Karsch, 1979. Neuroendocrine regulation of the estrous cycle and seasonal breeding in the ewe. Biol. Reprod. 20:74-85.

Lilburn, M. S., and D. J. Myers-Miller, 1990. Dietary effects on body composition and subsequent production characteristics in broiler breeder hens. Poultry Sci. 69:1126-1132.

Lopez, G., and S. Leeson, 1994. Nutrition and broiler breeder performance: a review with emphasis on response to diet protein. J. Appl. Poultry Res. 3:303-311.

Lopez, G., and S. Leeson, 1995. Response of broiler breeders to low-protein diets. 1. Adult breeder performance. Poultry Sci. 74:685-695.

Luther, L. W., W. W. Abbott, and J. R. Couch, 1976. Low lysine, low protein, and skip-a-day restriction of summer and winter reared broiler breeder pullets. Poultry Sci. 55:2240-2247.

Lynch, H. J., and C. L. Ralph, 1970. Diurnal variation in pineal melatonin and its non-relationship to HIOMT activity. Am. Zoologist 10: 300 (Abstract).

Marks, H. L., 1985. Direct and correlated responses to selection for growth. Br. Poult. Sci. 26: 47-57.

Marr, J. E., and F. W. Garland, Jr., R. C. Eaton, and H. L. Wilcke, 1962. Effect of controlled day length during the growing and laying periods on egg production. Poultry Sci. 41:1663 (Abstract).

McDaniel, G. R., J. Brake, and M. K. Eckman, 1981. Factors affecting broiler breeder performance. 4. Interrelationship of some reproductive traits. Poultry Sci. 60:1792-1797.

Menaker, M., R. Roberts, J. Elliott, and H. Underwood, 1970. Extra retinal light perception in the sparrow. III: The eyes do not participate in photoperiodic photoreception. Proc. Natl. Acad. Sci. 67: 320-325.

Miyamoto, K., Y. Hasegawa, T. Minegishi, M. Nomura, Y. Takahashi, M. Igarashi, K. Kanagawa and H. Matsuo, 1982. Isolation and characterization of chicken hypothalamic luteinizing hormone releasing hormone. Biochem. Biophys. Res. Comm. 107: 820-827.

Miyamoto, K., Y. Hasegawa, M. Nomura, M. Igarashi, K. Kanagawa, and H. Matsuo, 1984. Identification of the second gonadotropin-releasing hormone in the chicken hypothalamus: evidence that gonadotropin secretion is probably controlled by two distinct gonadotropin-releasing hormones in avian species. Proc. N.Y. Acad. Sci. 81: 3874-3878.

Moenter, S. M., C. J. I. Woodfill, and F. J. Karsch, 1991. Role of the thyroid gland in seasonal reproduction: thyroidectomy blocks seasonal suppression of reproductive neuroendocrine activity in ewes. Endocrinology 128:1337-1344.

Morris, T. R., 1967. Light requirements of the fowl. Pages 15-39 *in:* Environmental Control in Poultry Production. T. C. Carter, ed. Oliver and Boyd, Edinburgh.

Morris, T. R., and S. Fox, 1958. Light and sexual maturity in the domestic fowl. Nature 181:1453-1454.

Morris, T. R., S. Fox, and R. C. Jennings, 1964. The response of laying pullets to abrupt changes in daylength. Br. Poultry Sci. 5:133-147.

Morris, T. R., P. J. Sharp, and E. A. Butler, 1995. A test for photorefractoriness in high-producing stocks of laying pullets. Br. Poult. Sci. 36:763-769.

Mougdal, R. P., and M. N. Razdan, 1985. Induction of ovulation *in vitro* in the hen: dependency of the response to LH on age and rate of lay. J. Endocrinol. 106:67-69.

Nakahara, K., N. Murakami, T. Nasu, H. Kuroda, and T. Murakami, 1997. Individual pineal cells in chick possess photoreceptive, circadian clock and melatonin-synthesizing capacities *in vitro*. Brain Res. 774: 242-245.

National Research Council, 1984. Nutrient requirements of poultry. 8th rev. ed. National Academy Press, Washington, DC.

National Research Council, 1994. Nutrient requirements of poultry. 9th rev. ed. National Academy Press, Washington, DC.

Nicholls, T. J., A. R. Goldsmith, and A. Dawson, 1988. Photorefractoriness in birds and comparison with mammals. Phys. Reviews 68:133-176.

Ohkubo, T., M. Tanaka, K. Nakashima, R. T. Talbot, P. J. Sharp, 1998a. Prolactin receptor gene expression in the brain and peripheral tissues in broody and nonbroody breeds of domestic hen. Gen. Comp. Endocrinol. 109:60-68.

Ohkubo, T., M. Tanaka, K. Nakashima, P. J. Sharp, 1998b. Relationship between prolactin receptor mRNA in the anterior pituitary gland and hypothalamus and reproductive state in male and female bantams (*Gallus domesticus*). Gen. Comp. Endocrinol. 111:167-176.

Oksche, A., 1980. Structural organization of avian neuroendocrine systems. Pages 3-15 *in:* Biological Rhythms in Birds: Neural and Endocrine Aspects. Y. Tanabe, K. Tanaka, and T. Ookawa, ed. Japan Scientific Societies Press, Tokyo/Springer-Verlag, Berlin.

Oliver, J., and J. D. Bayle, 1976. Effects of local illumination of the hypothalamus on spontaneous and flash-induced multiunit activity recorded from gonadotropic hypothalamic areas in quail. J. Neurosci. Res. 2:449-456.

Oliver, J., and J. D. Bayle, 1982. Brain photoreceptors for the photo-induced testicular response in birds. Experientia 38:1021-1029.

Oliver, J., and M. Jallageas, and J. D. Bayle, 1979. Plasma testosterone and LH levels in male quail bearing hypothalamic lesions or radioluminous implants. Neuroendocrinology 28:114-122.

Parry, D. M., and A. R. Goldsmith, 1993. Ultrastructural evidence for changes in synaptic input to the hypothalamic luteinizing hormone-releasing hormone neurons in photosensitive and photorefractory starlings. J. Neuroendocrinol. 5:387-395.

Paug, S. F., G. M. Brown, L. J. Grota, J. W. Chambers, and R. L. Rodman, 1977. Determination of *N*-acetylserotonin and melatonin activities in the pineal gland, retina, Harderian Gland, brain and serum of rats and chickens. Neuroendocrinology 23:1-13.

Pearson, R. A., and K. M. Herron, 1981. Effects of energy and protein allowances during lay on the reproductive performance of broiler breeder hens. Br. Poult. Sci. 22:227-239.

Quay, W. B., 1965. Retinal and pineal hydroxyindole-O-methyl transferase activity in vertebrates. Life Sciences 4:983-991.

Reeves, J. J., P. C. Harrison, and J. M. Casey, 1973. Ovarian development and ovulation in hens treated with synthetic (porcine) luteinizing hormone releasing hormone / follicle stimulating hormone releasing hormone (LH-RH/FSH-RH). Poultry Sci. 52: 1883-1886.

Robinson, F. E., and R. J. Etches, 1986. Ovarian steroidogenesis during follicular maturation in the domestic fowl (*Gallus domesticus*). Biol. Reprod. 35: 1096-1105.

Robinson, F. E., T. A. Wautier, R. T. Hardin, N. A. Robinson, J. L. Wilson, M. Newcombe, and R. I. McKay, 1996. Effects of age at photostimulation on reproductive efficiency and carcass characteristics. 1. Broiler breeder hens. Can. J. Anim. Sci. 76:275-282.

Romanoff, A. L., and A. J. Romanoff, 1949. Formation. Pages 175-252 *in:* The Avian Egg. A. L. Romanoff and A. J. Romanoff, ed. John Wiley, New York, NY.

Sakurai, H., M. Kawashima, M. Kamiyoshi, and K. Tanaka, 1986. Effect of serotonin and β-endorphin on the release of luteinizing hormone in the hen (*Gallus domesticus*). Gen. Comp. Endocrinol. 63:24-30.

Scanes, C. G., 1984. Hypothalamic, pituitary and gonadal hormones. Pages 1-14 *in:* Reproductive Biology of Poultry. F. J. Cunningham, P. E. Lake, and D. Hewitt, ed. British Poultry Science Ltd., Longman Group, Harlow, England.

Scanes, C. G., A. Chadwick, P. J. Sharp, and N. J. Bolton, 1978. Diurnal variation in plasma luteinizing homorne levels in the domestic fowl (*Gallus domesticus*). Gen. Comp. Endocrinol. 34: 45-49.

Scanes, C. G., S. Harvey, A. Chadwick, L. Gales, and W. S. Newcomer, 1980. Diurnal variations in serum luteinizing hormone, growth hormone, and prolactin concentrations in intact and pinealectomized chickens. Gen. Comp. Endocrinol. 41: 266-269.

Shahabi, N. A., H. W. Norton, and A. V. Nalbandov, 1975. Steroid levels in follicles and the plasma of hens during the ovulatory cycle. Endocrinology 96: 962-968.

Sharp, P. J., 1984. Seasonal breeding and sexual maturation. Pages 203-218 *in:* Reproductive Biology of Poultry. F. J. Cunningham, P. E. Lake, and D. Hewitt, ed. British Poultry Science Ltd., Longman Group, Harlow, England.

Sharp, P. J., 1992. The photoperiodic responses of juvenile domestic hens. Ornis Scandinavica 23:411-415.

Sharp, P. J., 1993. Photoperiodic control of reproduction in the domestic hen. Poultry Sci. 72:897-905.

Sharp, P. J., I. C. Dunn, and S. Cerolini, 1992. Neuroendocrine control of reduced persistence of egg-laying in domestic hens: evidence for the development of photorefractoriness. J. Reprod. Fertil. 94:221-235.

Sharp, P. J., R. T. Talbot, G. M. Main, I. C. Dunn, H. M. Fraser, and N. S. Huskisson, 1990. Physiological roles of chicken LHRH-I and –II in the control of gonadotropin release in the domestic chicken. J. Endocrinol. 124:291-299.

Siegel, P. B., and E. A. Dunnington, 1985. Reproductive complications associated with selection for broiler growth. Br. Poult. Sci. 26: 59-72.

Silver, R., P. Witkovsky, P. Horvath, V. Alones, C. J. Barnstable, and M. N. Lehman, 1988. Coexpression of opsin-and VIP-like-immunoreactivity in CSF-contacting neurons of the avian brain. Cell Tiss. Res. 253: 189-198.

Singsen, E. P., and J. Nagel, S. G. Patrick, and L. D. Matterson, 1965. The effect of a lysine deficiency on growth characteristics, age at sexual maturity, and reproductive performance of meat-type pullets. Poultry Sci. 44:1467-1473.

Siopes, T. D., 1994. Critical day lengths for egg production and photorefractoriness in the domestic turkey. Poultry Sci. 73:1906-1913.

Siopes, T. D., and W. O. Wilson, 1980. Participation of the eyes in the photostimulation of chickens. Poultry Sci. 59:1122-1125.

Soller, M., T. Brody, Y. Eitan, T. Agurksy, and C. Wexler, 1984. Minimum weight for the onset of sexual maturity in female chickens: heritability and phenotypic and genetic correlations with early growth rate. Poultry Sci. 63:2103-2113.

Sreekumar, K. P., and P. J. Sharp, 1998. Effect of photostimulation on concentrations of plasma prolactin in castrated bantams (*Gallus domesticus*). J. Neuroendocrinol. 10:147-154.

Stansfield, S. C., and F. J. Cunningham, 1988. Attenuation of endogenous opioid peptide inhibition of [Gln^8]Luteinizing hormone-releasing hormone secretion during sexual maturation in the cockerel. Endocrinology 123:787-794.

Spratt, R. S., and S. Leeson, 1987. Broiler breeder performance in response to diet protein and energy. Poultry Sci. 66:683-693.

Summers, J. D., and S. Leeson, 1983. Factors influencing early egg size. Poultry Sci. 62:1155-1159.

Summers, J. D., and S. Leeson, 1993. Influence of diets varying in nutrient density on the development and reproductive performance of White Leghorn pullets. Poultry Sci. 72:1500-1509.

Sun, J.-H., R. J. Reiter, A. Hattori, K. Yaga, D. C. Herbert, A. T. C. Tsin, 1993. Phototransduction-related circadian changes in indoleamine metabolism in the chick pineal gland *in vivo*. J. Pineal Res. 15: 132-137.

Thrun, L.. A., G. E. Dahl, N. P. Evans, and F. J. Karsch, 1997. Effect of thyroidectomy on maintenance of seasonal reproductive suppression in the ewe. Biol. Reprod. 56:1035-1040.

van Tienhoven, A., A. V. Schally, 1973. Mammalian luteinizing hormone-releasing hormone induces ovulation in the domestic fowl. Gen. Comp. Endocrinol. 19: 594-595.

Waldroup, P. W., B. L. Damron, and R. H. Harms, 1966. The effect of low protein and high fibre grower diets on the performance of broiler pullets. Poultry Sci. 45:393-402.

Waldroup, P. W., K. R. Hazen, W. D. Bussell, and Z. B. Johnson, 1976. Studies on the daily protein and amino acid needs of broiler breeder hens. Poultry Sci. 55:2342-2347.

Wang, S. -C., and J. M. Bahr, 1983. Estradiol secretion by theca cells of the domestic hen during the ovulatory cycle. Biol. Reprod. 28: 618-624.

Wells, J. W., A. B. Gilbert, and J. Culbert, 1980. Effect of luteinizing hormone on progesterone secretion *in vitro* by the granulosa cells of the domestic fowl (*Gallus domesticus*). J. Endocrinol. 84: 249-254.

Williams, J. B., and P. J. Sharp, 1978a. Ovarian morphology and rates of ovarian follicular development in laying broiler breeders and commercial egg-producing hens. Br. Poult. Sci. 19: 387-395.

Williams, J. B., and P. J. Sharp, 1978b. Age-dependent changes in the hypothalamo-pituitary-ovarian axis of the laying hen. J. Reprod. Fertil. 53:141-146.

Wilson, S. C., and F. J. Cunningham, 1984. Endocrine control of the ovulation cycle. Pages 29-50 *in:* Reproductive Biology of Poultry. F. J. Cunningham, P. E. Lake, and D. Hewitt, ed. British Poultry Science Ltd., Longman Group, Harlow, England.

Wilson, S. C., and P. J. Sharp, 1973. Variations in plasma LH levels during the ovulatory cycle of the hen, *Gallus domesticus*. J. Reprod. Fert. 35: 561-564.

Wilson, S. C., and P. J. Sharp, 1975. Effects of progesterone and synthetic luteinizing hormone releasing hormone on the release of luteinizing hormone during sexual maturation in the hen (*Gallus domesticus*). J. Endocrinol. 67: 359-369.

Wilson, S. C., and P. J. Sharp, 1976. Induction of luteinizing hormone release by gonadal steroids in the ovariectomized domestic hen. J. Endocrinol. 71: 87-98.

Wilson, W. O., and A. E. Woodard, 1958. Egg production of chickens kept in darkness. Poultry Sci. 37:1054-1057.

Xiong, J. J., F. J. Karsch, and M. N. Lehman, 1997. Evidence for seasonal plasticity in the gonadotropin-releasing hormone (GnRH) system of the ewe: changes in synaptic inputs onto GnRH neurons. Endocrinology 138:1240-1250.

Yu, M. W., F. E. Robinson, and R. J. Etches, 1992. Quantification of ovarian steroidogenesis in the domestic fowl by incubation of intact large follicles. Poultry Sci. 71: 346-351.

Yuan, T., R. J. Lien, and G. R. McDaniel, 1994. Effects of increased rearing period body weights and early photostimulation on broiler breeder egg production. Poultry Sci. 73:792-800.

Zelenka, D. J., P. B. Siegel, E. A. Dunnington, and J. A. Cherry, 1986. Inheritance of traits associated with sexual maturity when populations of chickens reach 50% lay. Poultry Sci. 65:233-240.

2.0 EFFECT OF DIETARY PROTEIN INTAKE DURING THE PULLET-TO-BREEDER TRANSITION PERIOD ON EARLY EGG WEIGHT AND PRODUCTION IN BROILER BREEDERS

2.1 INTRODUCTION

According to the National Research Council (NRC), chickens do not require an absolute level of crude protein (CP) in their diet (NRC, 1994). However, some level of protein must be included in the diet in order to provide both essential and nonessential amino acids and amino nitrogen for the synthesis of nonessential amino acids (NRC, 1994). In the case of broiler and commercial layer operations, *ad libitum* consumption of feed ensures that the bird receives an adequate amount of protein to satisfy its needs. For broiler breeders, feed restriction is necessary in order to control body weight (BW) because it can improve egg weight and egg production (Siegel and Dunnington, 1985). Unfortunately, an appropriate level of crude protein for broiler breeders has not been determined. Several studies have shown that protein levels of 10 to 14% CP (with supplemental essential amino acids) satisfy the protein requirement of hens already in lay (Waldroup et al., 1976; Bornstein et al., 1979; Lopez and Leeson, 1995). Bowmaker and Gous (1989) calculated that a broiler breeder pullet would require approximately 10 g of CP per day before the onset of lay, in addition to the amount needed to sustain egg production.

Breeder companies often suggest having as high as 15 to 16% CP in the breeder diet. The Cobb 500 Breeder Management Guide recommends that early intake of protein leads to improved flock uniformity (Anonymous, 1998). As the bird ages, additional protein serves to maintain flock uniformity and ensure a proper degree of fleshing on the bird. A high level of dietary protein also maximizes the amount of carcass protein available for egg formation and egg production. In practical terms it would be useful to know what the appropriate amount of crude protein should be in the breeder diet. Most studies with meat-type pullets have reported beneficial effects of increasing protein in the diet, in terms of egg production and egg weight. A linear increase in egg weight and the rate of egg production was noted as the amount of dietary protein, fed from 24 to 56 weeks (wk) of age, increased from 14.5 to 22 g/day (d) in the hen diet (Waldroup et al., 1976). However, a protein level of 24 g/d did not result in any further increases in egg production (Waldroup et al., 1976). Cave (1984) and Brake et al. (1985) attributed the increase in egg production in their trials to an increase in protein deposition in the body. Bowmaker and Gous (1989) also found that egg production was increased in their trial because of increased protein in the diet.

Although these previous studies report beneficial effects of increased dietary protein on egg production, there is not enough evidence to conclude that current high breast yield birds would respond similarly as did broiler breeders 10 to 15 years ago. It is possible that there is a limit to the effect of increasing dietary CP on egg weight and egg production (Fisher, 1998). Pearson and Herron (1981) found those diets containing more than 63 g of protein per Mcal AME reduced egg production and hatchability in broiler breeders. Dietary protein beyond this upper limit may actually increase BW as broiler breeders today have been selected for rapid growth and increased breast muscle mass. Increased BW in broiler breeders has been shown to increase the rate of follicular maturation (Siegel and Dunnington, 1985). In other words, there are more ovulations than the oviduct can process into single intact eggs. The end result is the production of defective eggs that are unfit for setting in incubators. The objective of the present trial was to study the effect of three dietary CP levels in a prelay and early lay diet on reproductive performance of high breast yield broiler breeders, including egg weight, egg production, and egg quality and carcass composition. The hypothesis tested was that a high protein diet would increase egg size and egg production as compared to a low protein diet. The second hypothesis was that additional protein beyond 16% CP would only result in increased BW.

2.2 MATERIALS AND METHODS

Stocks and Management

The University of Alberta's Faculty of Agriculture, Forestry and Home Economics Animal Policy and Welfare Committee approved this protocol according to the *Guide to the Care and*

Use of Experimental Animals (Canadian Council on Animal Care, 1984). A flock of 300 commercial broiler breeder pullets[1] were reared in floor pens (1.38 ft^2/bird) in a light-tight facility under 24 hours (h) of light/d for the first 3 d post hatch and then 8 h of light/d to 22 wk of age. From hatch to 3 wk of age, the pullets received a standard starter diet (2.78 Mcal ME/kg; 18.21% CP) fed *ad libitum*. At 3 wk of age, they were changed to a grower diet (2.71 Mcal ME/kg; 15.04% CP). Feed allocation was based on the mean weekly BW as recommended by the Cobb 500 Breeder Management Guide and followed a skip-two-day feeding schedule (Anonymous, 1998). That is to say, the birds were fed for 3 d (Monday to Wednesday), not fed for 1 d (Thursday), fed for 2 d (Friday and Saturday) and not fed another day (Sunday). The entire schedule was then repeated. The amount of feed to be allocated was calculated by multiplying the daily consumption by 7 d to get the total amount of feed allocated over 1 wk. This amount of feed was then divided by 5 d to determine the amount of feed to determine the amount of feed to given on the skip-two-day program. Each week when the feed allocation was determined the amount was recalculated accordingly.

Experimental Design

At 20 wk of age, each pullet was weighed and the 96 birds closest to the target BW (2.160 kg), as recommended by the breeder guide, were selected (Anonymous, 1998). These birds were then randomly placed into individual laying cages in another light-tight facility. At 20 wk of age, each bird was assigned to one of three treatments. The diets contained one of 14, 16, or 18% dietary CP (Table 2-1). The 16% CP treatment was treated as the standard level of CP for this trial. The diets were formulated to be isocaloric and supplemental amino acids were added in proportion to the crude protein level. Feed allocation was identical for all three treatments and was based on the average weekly BW of the pullets fed the 16% CP diet.

Egg Weight and Production. Photostimulation occurred at 22 wk of age when the photoperiod was increased to 14 h of light/d. At first oviposition (considered to be the time of sexual maturity), the age and BW of the hens were recorded. Individual daily records of egg production and egg weight were recorded for the determination of weekly and total egg production and egg mass. The total production period was calculated from the day the first egg in the flock was collected (across all treatments) to the day prior to processing. Egg weight was recorded and an egg quality code was assigned. An egg with an intact shell and a single yolk, regardless of weight, was defined as a normal egg. A settable egg was classified as a normal egg that was more than 52 g in weight. Eggs that did not fit into either group were considered defective. At the end of each week, the two most recent eggs laid from each hen were used to determine egg characteristics. These eggs were weighed (post storage) and then opened. The yolk was separated from the albumen. The shells were washed with tap water to remove adhering albumen and air-dried at room temperature for four days. Yolk and shell were individually weighed. Albumen weight was obtained by subtracting the yolk and shell weights from egg weight.

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[1] Cobb 500, slow feathering strain. From Cobb-Vantress Inc., Siloam Springs, AR, USA

Carcass and Ovarian Characteristics. At 29 wk of age, birds were killed by cervical dislocation and then weighed individually. The *Pectoralis major* and *Pectoralis minor*, liver, abdominal fat pad, oviduct, and ovary were removed and individually weighed. Contents in the oviduct were removed before the oviduct was weighed. The ovary was analyzed for follicular development. Any follicles greater then 10 mm in diameter (large yellow follicles; LYF) were individually weighed. The LYF were sorted by order of largest to smallest weight with the term 'F1' given to the largest follicle as it is, presumably, the one to ovulate first. Follicles measuring 5 to 10 mm in diameter (small yellow follicles; SYF) were counted and recorded. Any incidence of LYF or SYF follicular atresia was noted.

Carcass Composition. After the organs and tissues were weighed, they were returned to the bird carcass and stored at –15 C. Carcass composition was carried out on fully feathered birds with all carcass components. In preparation for body composition analysis, thawed carcasses were placed in individual pressure cookers and cooked for 4 h. Once softened, the entire contents of the pressure cooker were emptied into an industrial blender and then homogenized. Two 200 g samples of the homogenate were freeze-dried and then ground using a commercial blender. The ground samples were analyzed for the amount of dry matter, total protein (N × 6.25), total lipid, and total ash using standard procedures of the Association of Official Analytical Chemists (1980). The values were adjusted for moisture content as described previously (Renema et al., 1999).

Statistical Analysis

Pullets were assigned to a dietary CP level and a cage in a completely randomized design. Data were evaluated by one-way analysis of variance using the General Linear Models procedures of SAS® (SAS Institute, 1994) with dietary CP level as the main effect. Following a significant F-test *($P \leq 0.05$)*, differences between means were evaluated with the PDIFF T-Test procedure of SAS® (SAS Institute, 1994). The error variation for protein level was the variation between birds. Egg weight and production data was summarized for each bird on a weekly and total egg production basis using the PROC MEANS procedure of SAS® (SAS Institute, 1994). Pearson correlation coefficients were completed on the carcass composition data (Steel et al., 1997). One bird was culled from the 14% CP group therefore, SEM values were based on this group. Unless otherwise stated, all statements of significance were based on testing at the $P \leq 0.05$ level.

2.3 RESULTS AND DISCUSSION

Body Weight and Body Weight Gain

Body weight did not change significantly as a result of increasing the CP level (Table 2-2). Studies have noted that the mature BW of a broiler breeder hen was more influenced by energy rather than protein intake (Keshavarz and Nakajima, 1995; Spratt and Leeson, 1987). It is possible that the birds in the present trial had already achieved a mature BW before the trial started, therefore, differences in protein content in the diet would have had a minimal effect. Body weight gain throughout the 20-29 wk period was not significantly different among treatments (data not shown). Harms and Russell (1995) reported that BW gain decreased as dietary protein decreased. However, their study involved breeder hens that were past the age of peak egg production and the potential for differences in BW gain are greater as the bird ages because fat deposition increases and nutrient requirements for egg formation decrease (Lopez and Leeson, 1994). Like BW, the age at sexual maturity was not different among the treatments (176.9 ± 1.0, 177.3 ± 1.0, and 174.6 ± 1.0 d, post lighting for 14, 16, and 18% CP, respectively).

Egg Weight

Feeding higher levels of dietary protein to broiler breeder hens resulted in the production of larger eggs when compared to the birds fed 14% CP (Table 2-3). From 25 to 28 wk of age, birds on the 16 and 18% CP treatments produced a consistently higher mean egg weight than the 14% CP treatment ($P = 0.0001$). There were no significant differences in egg weight between the 16% CP and 18% CP treatments. In response to increased dietary protein, differences in egg weight were only found at 60 wk of age (Lopez and Leeson, 1995). In the current study, there was no difference between CP treatments on egg weight at 29 wk of age. However, mean egg weight over the laying period of this trial, from 24 to 29 wk of age, was significantly higher in the 16 and 18% CP treatments when compared to the 14% CP treatment, suggesting that the additional protein benefited early egg size.

The increase in mean egg weight by the 16 and 18% CP treatments was mainly a result of increased albumen weight (Table 2-3), which differed significantly from the 14% CP treatment (32.0 ± 0.2, 33.7 ± 0.2, and 33.3 ± 0.2 g, for 14, 16, and 18% CP, respectively). Mean yolk weight was unaffected by protein level (12.8 ± 0.1, 12.7 ± 0.1, and 12.8 ± 0.1 g, for 14, 16, and 18% CP, respectively). Shell weight significantly higher in the 18% CP treatment (4.56 ± 0.07, 4.54 ± 0.07, and 4.73 ± 0.07 g, for 14, 16, and 18% CP, respectively). The increase in albumen weight was supported by other studies (Fisher, 1969; Keshavarz and Nakajima, 1995). Butts and Cunningham (1972) noted that the total nitrogen content in the albumen increased as dietary protein increased. Total egg mass output, defined as the cumulative weight of all of the eggs laid per hen, was not affected by protein level (Table 2-4). Higher levels of protein have been shown to increase early egg weight in layers because BW was also increased (Summers, 1993; Summers and Leeson, 1994). However, the increase in egg weight was not accompanied by an increase in BW in this trial.

Egg Production

Although there was no difference in egg weight at 29 wk of age, the rate of egg production in the 14% CP group fell below that of the hens on the 16 and 18% CP diets (Table 2-3). The lowest level of protein in the diet, (14% CP) was, presumably, inadequate as it was unable to sustain as high a level of egg production as the other two treatments. An early indication of this difference occurred at 25 wk of age when the 18% CP group had 65.2% hen-day egg production as compared to 49.8% hen-day egg production in the lowest dietary protein group. Interestingly, the 16% CP group also produced fewer eggs than the 18% CP at 25 wk of age but by 29 wk no difference was observed. Brake et al. (1985) reported an increase in egg production in hens fed additional protein. In another study, increased egg production during the early lay period was noted in hens fed a high protein prelay diet (Lilburn and Myers-Miller, 1990). Over the 5-wk laying period (24 to 29 wk of age), egg production was not different.

Egg numbers, in the present study, were divided into categories (normal, settable, and total) based on the code that each egg was given at the time of collection (Table 2-4). Although the number of normal eggs was not different among the treatments, the number of settable eggs (over 52 g in weight) were highest in the higher protein treatments. On a per bird basis, the birds fed 18% CP produced four additional settable eggs than the birds on the 14% CP treatment. The number of settable eggs was not different between the 16 and 18% CP treatments. The difference in weekly hen-day egg production between 16 and 18% CP groups at 25 wk of age was mainly a result of an increased number of double-yolked and membranous eggs in the 18% CP treatment.

Carcass and Ovarian Characteristics

There was no difference in BW at processing (29 wk of age) among treatments (Table 2-5). Dietary protein did not affect the weight of either the *Pectoralis major* or *Pectoralis minor*. Liver weight and abdominal fat pad weight at processing was also not influenced by the level of CP in the prelay and early lay diet. Lilburn and Myers-Miller (1990) reported a decrease in fat pad weight and an increase in *Pectoralis major* weight when the dietary protein level was increased from 16 to 23%, which is a higher level of crude protein than what was investigated in this trial. The birds fed 14% CP also averaged 0.26 atretic LYF per bird and this average differed significantly from the 18% CP group, which had no signs of LYF atresia. Atresia at the LYF level of follicular maturation is uncommon, especially in young birds. However, when it does occur it is usually associated with a decrease in the number of LYF available to ovulate, and subsequently, the number of eggs. Although there were no differences in the number of LYF, the high number of atretic LYF in the 14% CP may have contributed to the decrease in egg production in that treatment at 29 wk of age. However, there were no subsequent differences in ovary weight, LYF weight, or the number of SYF. Likewise, dietary protein did not affect the average or total weight of the LYF or the weight of the F1 follicle.

Carcass Composition

The carcass composition data are presented in Table 2-6. Despite differences in egg production, the carcass moisture, protein, lipid and ash levels were similar among all treatments. Correlation analysis did not show any significant relationships. Brake et al. (1985) attributed the CP intake effect in their trial to increased protein stores in the body. The results from the present study did not agree with those findings. Cave (1984) suggested that increased dietary protein resulted in a hypertrophy of the liver explaining the increase in egg production in that study. The findings of Bowmaker and Gous (1989) and the present study show that liver weight was not affected by the amount of dietary protein. Therefore, the increase in egg production parameters noted in this study does not support the interpretation that increased levels of dietary protein lead to increased protein retention in the body. Rather than an increase in protein stores, the present study suggests that the additional nitrogen content in the 16 and 18% CP diets was diverted directly into egg formation. Hens that received more protein in the diet produced larger eggs because they were given proportionately more essential amino acids than the hens on the 14% CP treatment. The increase in albumen weight in the eggs from the higher protein treatments supports this view.

Feeding the lowest level of dietary protein (14% CP) in this trial had no effect on BW or breast muscle deposition; however, egg size and egg production were significantly reduced. Increasing the level of protein to either 16 or 18% CP resulted in increased mean egg weight and increased mean egg production, suggesting that the additional protein was partitioned towards reproduction. Manipulating energy intake in order to increase egg weight and egg production is difficult, as BW will also be increased. This study demonstrated that positive increases in egg weight and egg production were achieved by altering the protein level without affecting BW, even in broiler breeders that are selected for larger breast muscle mass. In terms of 16% versus 18% CP, there were no large differences in mean egg weight or in normal and settable egg production. Therefore feeding a higher level of protein (18% CP) during the pullet-to-breeder transition period was not effective as similar results were achieved by feeding the 16% CP diet. After peak egg production, broiler breeder hens typically consume more nutrients than are processed into eggs. Therefore, it would have been interesting to determine the effects of feeding 14, 16, and 18% CP levels over an entire broiler breeder production cycle.

Table 2-1. The composition and nutrient intake of the experimental diets given to the female broiler breeders during the pullet-to-breeder transition period (20 to 29 wk of age)

	Dietary protein		
Ingredient	14% CP	16% CP	18% CP
	(%)		
Ground corn	66.70	65.88	64.21
Soybean meal (44% CP)	13.23	16.56	17.38
Oats	4.00	2.00	1.00
Wheat, hard red winter	4.00	2.16	1.49
Meat meal	1.20	2.40	4.80
Corn gluten meal	0.60	1.20	2.40
Canola oil	0.89	0.91	0.76
Dicalcium phosphate	1.62	1.25	0.59
Ground limestone	6.36	6.23	5.96
Choline chloride premix[1]	0.50	0.50	0.50
Layer premix[2]	0.50	0.50	0.50
Salt	0.36	0.36	0.35
D, L-methionine	0.05	0.06	0.06
Nutrient composition			
CP (analyzed), %	14.8	16.4	18.5
ME (analyzed), Mcal per kg	2.76	2.83	2.84
Calcium (analyzed), %	3.13	2.63	3.17
Available phosphorus (calculated), %	0.45	0.42	0.38
Methionine (calculated), %	0.28	0.32	0.36
Lysine (calculated), %	0.67	0.78	0.86

[1] Choline chloride premix was supplied at a level of 100 mg per kilogram of diet.

[2] Layer premix supplied the following per kilogram of diet: vitamin A, 12,000 IU; vitamin D3, 3,000 IU; vitamin E, 40 IU; vitamin K, 2.0 mg; pantothenic acid, 14 mg; riboflavin 6.5 mg; folacin, 1.0 mg; niacin, 40 mg; thiamine, 3.3 mg; pyridoxine, 6.0 mg; vitamin B_{12}, 0.02 mg; biotin, 0.2 mg; iodine, 0.5 mg; Mn, 75 mg; Cu, 15 mg; Zn, 80 mg; Se, 0.1 mg; Fe, 100 mg.

Table 2-2. Mean weekly BW and feed allocation for female broiler breeders fed one of three levels of dietary protein

		Age (wk)									
Variable	Treatment	20	21	22	23	24	25	26	27	28	29
BW		(kg)									
	14% CP	1.964	2.095	2.314	2.472	2.641	2.813	2.894	2.958	2.987	3.132
	16% CP	1.929	2.071	2.304	2.480	2.650	2.818	2.921	2.985	3.019	3.153
	18% CP	1.958	2.099	2.348	2.497	2.682	2.867	2.943	3.003	3.044	3.183
	SEM	0.024	0.024	0.021	0.023	0.024	0.027	0.030	0.033	0.033	0.035
Feed allocation		(g/day)									
Total	All birds	100	107	110	116	122	125	130	135	141	144
Dietary CP	14% CP	14.8	15.8	16.3	17.2	18.1	18.5	19.2	20.0	20.9	21.3
	16% CP	16.4	17.5	18.0	19.0	20.0	20.5	21.3	22.1	23.1	23.6
	18% CP	18.5	19.8	20.0	21.5	22.3	23.1	24.1	25.0	26.1	26.6

Table 2-3. The effect of protein level in the prelay and early lay diet on mean weekly egg weight and egg production of broiler breeder females (24 to 29 wk of age)

		Age (wk)						
Variable	Treatment	24	25	26	27	28	29	24 to 29
					(g)			
Egg weight								
	14% CP	44.9	46.8^{b}	49.2^{b}	51.9^{b}	53.5^{b}	54.2	50.1^{b}
	16% CP	45.9	48.7^{a}	50.9^{a}	52.9^{a}	54.3^{a}	55.1	51.3^{a}
	18% CP	45.8	48.6^{a}	51.4^{a}	53.5^{a}	54.5^{a}	55.3	51.5^{a}
	SEM	0.7	0.4	0.3	0.3	0.3	0.4	0.2
Albumen weight								
	14% CP	28.1	30.1^{b}	31.4^{b}	33.5	34.2^{b}	34.9	32.0^{b}
	16% CP	34.2	32.3^{a}	32.5^{a}	34.1	35.4^{a}	35.8	33.7^{a}
	18% CP	30.7	31.3^{ab}	32.6^{a}	34.3	35.3^{a}	35.6	33.3^{a}
	SEM	3.4	0.6	0.4	0.3	0.3	0.4	0.2
Egg production					(%)			
	14% CP	12.9	49.8^{b}	74.2	82.5	87.1	74.2^{b}	57.7
	16% CP	14.7	52.2^{b}	76.8	88.8	87.5	89.6^{a}	61.2
	18% CP	20.1	65.2^{a}	82.1	87.1	90.2	86.5^{a}	65.2
	SEM	4.2	4.2	4.2	4.2	4.2	4.2	2.4

^{a,b}Means within a column with no common superscript differ significantly ($P \leq 0.05$).

Table 2-4. The effect of protein level in a prelay and early lay diet on total egg weight[1] and egg production performance per hen from 24 to 29 wk of age

Variable	Dietary protein			
	14% CP	16% CP	18% CP	SEM
Total egg weight (g)	1,272.8	1,340.9	1,449.9	53.4
Total egg number				
Normal eggs[2]	21.8	23.6	24.6	1.1
Settable eggs[3]	9.4^b	13.6^a	13.8^a	1.3
All eggs[4]	24.0	25.2	27.5	1.0

[1] Total egg weight = the cumulative weight of all eggs laid per bird throughout the trial.

[2] Normal egg = an egg with a normal, intact shell and a single yolk.

[3] Settable egg = an egg that has a normal, intact shell, a single yolk, and a weight ≥ 52 g.

[4] All eggs = normal and defective (double-yolk, soft-shell, membranous, etc.) eggs.

[a,b] Means within a row with no common superscript differ significantly ($P \leq 0.05$).

Table 2-5. Carcass characteristics of female broiler breeders at 29 wk of age fed one of three levels of dietary protein during the prelay and early lay period (20 to 29 wk of age)

	Dietary protein			
Variable	14% CP	16% CP	18% CP	SEM
BW at processing[1] (kg)	3.132	3.153	3.183	0.035
Breast weight[2] (g)	543.7	557.0	570.9	11.2
Pectoralis major weight (g)	413.2	421.0	434.5	8.7
Pectoralis minor weight(g)	130.4	136.0	136.4	3.3
Liver weight (g)	61.7	60.9	58.3	1.8
Abdominal fat pad weight	72.7	61.0	65.0	3.5
Ovary weight (g)	71.2	72.5	70.0	1.5
Oviduct weight (g)	57.5	56.2	58.3	2.0
Stroma weight (g)	9.4	8.3	8.7	0.3
Ovarian parameters				
Number of SYF[3]	12.7	11.2	12.8	0.8
Number of LYF[4]	6.3	6.3	6.6	0.2
Number of atretic SYF	1.13	1.59	0.91	0.27
Number of atretic LYF	0.26[a]	0.06[ab]	0.00[b]	0.09
F1[5] weight (g)	14.0	14.1	14.2	0.2
Average weight of LYF	7.7	7.8	7.6	1.9
Total weight of LYF (g)	48.4	48.4	50.8	0.2

[1] BW at processing = BW after the bird was killed.

[2] Breast weight = sum of the *Pectoralis major* and *Pectoralis minor* weights.

[3] SYF = small yellow follicles (between 5 to 10 mm in diameter).

[4] LYF = large yellow follicles (greater than 10 mm in diameter).

[5] F1 = LYF on the ovary with the highest weight.

[a,b] Means within a row with no common superscript differ significantly ($P \leq 0.05$).

Table 2-6. The effect of protein level in the prelay and early lay diet on the body composition of a broiler breeder hen as expressed as a percentage of the total carcass

	Dietary protein			
Variable	14% CP	16% CP	18% CP	SEM
	(%)			
Moisture	59.42	60.82	60.53	0.53
Protein	20.33	20.63	20.47	0.25
Lipid	14.85	13.74	14.20	0.45
Ash	3.23	3.25	3.03	0.08

2.4 REFERENCES

Anonymous, 1998. The Cobb 500 Breeder Management Guide. Cobb-Vantress Inc., Siloam Springs, AR.

Association of Official Analytical Chemists, 1980. Official methods of analytical chemists. 13th ed. AOAC, Arlington, VA.

Bornstein, S., S. Hurwitz, and Y. Lev, 1979. The amino acid and energy requirements of broiler breeder hens. Poultry Sci. 58:104-116.

Bowmaker, J. E., and R. M. Gous, 1989. Quantification of reproductive changes and nutrient requirements of broiler breeder pullets at sexual maturity. Br. Poult. Sci. 30:663-675.

Brake, J., J. D. Garlich, and E. D. Peebles, 1985. Effect of protein and energy intake by broiler breeders during the prebreeder transition period on subsequent reproductive performance. Poultry Sci. 64:2335-2340.

Butts, J. N., and F. E. Cunningham, 1972. Effect of dietary protein on selected properties of the egg. Poultry Sci. 51:1726-1734.

Canadian Council on Animal Care, 1984. Guide to the Care and Use of Experimental Animals. Vol. 2. Canadian Council on Animal Care, Ottawa, ON, Canada.

Cave, N. A. G., 1984. Effect of a high-protein diet fed prior to the onset of lay on performance of broiler breeder pullets. Poultry Sci. 63:1823-1827.

Fisher, C., 1969. The effects of a protein deficiency on egg composition. Br. Poult. Sci. 10:149-154.

Fisher, C. 1998. Amino acid requirements of broiler breeders. Poultry Sci. 77:124-133.

Harms, R. H., and G. B. Russell, 1995. A re-evaluation of the protein and lysine requirements for broiler breeder hens. Poultry Sci. 74:581-585.

Keshavarz, K., and S. Nakajima, 1995. The effect of dietary manipulations of energy, protein, and fat during the growing and laying periods on early egg weight and egg components. Poultry Sci. 74:50-61.

Lilburn, M. S., and D. J. Myers-Miller, 1990. Dietary effects on body composition and subsequent production characteristics in broiler breeder hens. Poultry Sci. 69:1126-1132.

Lopez, G., and S. Leeson, 1994. Nutrition and broiler breeder performance: a review with emphasis on response to diet protein. J. Appl. Poultry Res. 3:303-311.

Lopez, G., and S. Leeson, 1995. Response of broiler breeders to low-protein diets. 1. Adult breeder performance. Poultry Sci. 74:685-695.

National Research Council, 1994. Nutrient Requirements of Poultry. 9th rev. ed. National Academy Press, Washington, DC.

Pearson, R. A., and K. M. Herron, 1981. Effects of energy and protein allowances during lay on the reproductive performance of broiler breeder hens. Br. Poult. Sci. 22:227-239.

Renema, R. A., F. E. Robinson, M. Newcombe, and R. I. McKay, 1999. Effects of body weight and feed allocation during sexual maturation in broiler breeder hens. 1. Growth and carcass characteristics. Poultry Sci. 78:619-628.

SAS Institute, 1994. The SAS System for Windows 3.11 Release 6.10. SAS Institute Inc., Cary, NC.

Siegel, P. B., and E. A. Dunnington, 1985. Reproductive complications associated with selection for broiler growth. Pages 59-72 *in*: Poultry Genetics and Breeding. W. G. Hill, J. M. Manson, and D. Hewitt, ed. British Poultry Science, Ltd., Harlow.

Spratt, R. S., and S. Leeson, 1987. Broiler breeder performance in response to diet protein and energy. Poultry Sci. 66:683-693.

Steel, R. G. D., J. H. Torrie, and D. A. Dickey, 1997. Principles and Procedures of Statistics: A Biometrical Approach. 3rd ed. WCB McGraw Hill Inc., New York, NY.

Summers, J. D., 1993. Influence of prelay treatment and dietary protein level on the reproductive performance of White Leghorn hens. Poultry Sci. 72:1705-1713.

Summers, J. D., and S. Leeson, 1994. Laying hen performance as influenced by protein intake to sixteen weeks of age and body weight at point of lay. Poultry Sci. 73:495-501.

Waldroup, P. W., K. R. Hazen, W. D. Bussell, and Z. B. Johnson, 1976. Studies on the daily protein and amino acid needs of broiler breeder hens. Poultry Sci. 55:2342-2347.

3.0 MAXIMIZING EARLY EGG SIZE IN BROILER BREEDER FEMALES BY DELAYING AGE AT PHOTOSTIMULATION

3.1 INTRODUCTION

Sexual maturation of broiler breeders is dependent on achieving the miminum thresholds of age, BW, and body composition (Brody et al., 1984; Zelenka et al., 1986; Katanbaf et al., 1989). Several studies have shown that feed restricted meat-type pullets must achieve a minimum BW and body composition level, rather than a minimum age, before sexual maturation can occur (Leeson and Summers, 1983; Soller et al., 1984; Katanbaf et al., 1989). Therefore, there is no advantage to photostimulating a broiler breeder flock too early, as sexual maturity will not be advanced in these feed restricted birds. A successful lighting program will involve stimulating sexual maturation when the BW and body composition requirements have been met. Broiler breeder pullets that were photostimulated at 14 wk of age commenced lay at the same time as pullets photostimulated 3 wk later (Yuan et al., 1994). Likewise, Robinson et al. (1996) found that photostimulating broiler breeders 20 d earlier did not result in earlier sexual maturity. Although birds may achieve hypothalamic maturation at a young age, they may not have the minimum BW or body composition necessary for sexual maturity (Robinson et al., 1993). Therefore delaying photostimulation is beneficial as it allows more time for the bird to attain an appropriate body size. An added benefit is that flock uniformity is improved as more birds achieve physical maturity; therefore, they can respond to the photostimulation cue simulateously (Hocking, 1996). Robinson et al. (1996) noted that when pullets were photostimulated at 160 d of age the number of days between photostimulation and sexual maturity and variability in BW at first egg were significantly reduced compared to pullets photostimulated at 150 d of age. Prior to being photostimulated at 160 d of age, the birds had already begun partitioning energy towards those organs involved in reproductive function. Thus, once these hens were photostimulated sexual maturation progressed rapidly (Robinson et al., 1996).

With advancements in growth rate and breast muscle yield, broiler chickens can achieve a mature frame size (i.e. 2 kg BW) at as young as 39 d of age. However, Eitan and Soller (1996) demonstrated that broiler breeders selected for a high threshold BW at sexual maturity took longer to initiate egg production than did birds selected for a low threshold BW. Presumably, the difference in response was caused by a weaker photoperiodic drive in the heavy weight breeders (Eitan and Soller, 1996). This raises the question, has genetic selection for increased meat yield in the broiler delayed the age at sexual maturity in the broiler breeder?

The first objective of this trial was to determine the effect of photostimulating at 20 versus 23 wk of age on the carcass and reproductive parameters of female broiler breeders. Although the industry has moved towards delaying photostimulation from 18 to 20 wk of age, it now seems that with faster broiler growth rates an even further delay is necessary. The second objective was to determine if the timing of sexual maturation (as affected by age at photostimulation) differs for three genotypes of Arbor Acres birds selected for different rates of growth and breast yield. The first strain (Arbor Acres Classic) is a commercial breeder strain selected for egg production and is designed for the consumer who wants both a 'whole-bird' and a 'de-boned' product. This strain is considered to be the closest to a 'female-line' of the three strains. The Arbor Acres Feather Sexable Yield (FSY), is a slow feathering strain also selected for egg production but with more breast muscle yield than the Classic strain. This strain is for the consumer who specifically wants a de-boned product. The third strain (EXP) is an experimental line that is not commercially available. It has been selected for more breast muscle yield than the FSY. This is the most modern broiler strain of the three as the broiler industry begins to focus more on the de-boned market, therefore, this strain is for the consumer who wants white meat yield at the lowest possible cost. The first hypothesis was that delaying photostimulation would delay the age at first oviposition but the rate at which sexual maturity occurred would be higher. That is, more birds would be adequately prepared for reproductive function and would respond to the lighting cue more uniformly. The second hypothesis was that the three strains would respond differently to delaying photostimulation, as presumably, differences in genetic selection criteria would result in differences in carcass and reproductive characteristics. If selection for high breast yield results in slower maturation, as was found with selection for high BW (Eitan and Soller, 1996), it was possible that delaying photostimulation to 23 wk of age would allow the EXP strain more time to complete growth. Thus the delay in photostimulation would benefit the EXP pullets more than Classic or FSY pullets.

3.2 MATERIALS AND METHODS

Stocks and Management

The University of Alberta's Faculty of Agriculture, Forestry and Home Economics Animal Policy and Welfare Committee approved this protocol according to the *Guide to the Care and Use of Experimental Animals* (Canadian Council on Animal Care, 1984). Two hundred forty pullets of each strain were obtained from Arbor Acres Farms Inc. [1] The birds were reared in 12 floor pens with 60 birds per pen in a light-tight facility. From 0 to 3 d of age, the chicks received 24 h of light/d. From 4 d to 19 wk of age the photophase was shortened to 8 h of light/d. For the first 3 wk post hatch, the pullets were given a starter diet fed *ad libitum* (ME: 2783 kcal/kg; CP: 18.1%). At 3 wk of age, the pullets were then fed a grower diet (ME: 2711 kcal/kg; CP: 14.6%) and fed according to a skip-two-day feeding schedule. Each week when BW was determined, feed allocation was recalculated accordingly. Feed ingredients and nutrient composition of the starter and grower diets are shown in Table 3-1.

Individual BW were taken at 28-d intervals beginning at 4 wk of age. When individual BW's were not taken, a group weight was taken at weekly intervals starting at 5 wk of age per pen in order to determine a mean weekly BW. Feed allocation was therefore based on the weekly BW for that pen as it compared to the Arbor Acres Broiler Breeder Management Manual (Anonymous, 1998). All strains were fed according to the FSY body weight curve to reduce variability in BW at the time the trial commenced.

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[1] Arbor Acres Farms Inc., 439 Marlborough Road, Glastonbury, CT, 06033, USA.

Experimental Design

Experimental Fate. At 18 wk of age, 86 pullets from each strain were selected for the trial. The birds were selected based on how close BW matched the target BW for 18 wk of age (1.820 kg) as recommended by the Arbor Acres Broiler Breeder Management Manual (Anonymous, 1998). Pullets from each of the three strains were then randomly assigned to one of two experimental fates (A or C). The A birds (38 of each strain) were euthanatized by cervical dislocation at 19 wk of age, to assess strain differences in carcass and ovarian morphology prior to photostimulation. The C birds (48 of each strain) were randomly placed into individual laying cages at 19 wk of age in a light-tight facility. At this time, black polyethylene plastic was placed down the center of the room dividing the room into two halves. Light-tight ducting enabled air circulation between the two sides of the room. This ensured that despite the division of the room, the environment for all of the birds was very similar. At 20 wk of age, one-half of the birds were photostimulated by increasing the day length from 8 h of light/d to 15 h of light/d. The other half remained on 8 h of light/d until 23 wk of age when they received the same increase in photoperiod. At this time the black curtain was removed. The cages were equipped with individual feeders. Feed was allocated daily from 19 wk of age and was based on the mean weekly BW of the entire flock.

At 19 wk of age the C birds were fed a pre-breeder diet (ME: 2900 kcal/kg of diet; 16.5% CP). At 30 wk of age an error in the feed ration was discovered. The pre-breeder diet was deficient in calcium (1.34%). The ration was immediately supplemented with oystershell. A new breeder ration (ME: 2900 kcal/kg of diet; 16.1% CP) with the appropriate level of calcium (2.95%) was fed to the birds beginning at 31 wk of age. The pre-breeder and breeder diets are listed in Table 3-2. The birds remained on this ration until 53 wk of age, when the trial was terminated.

Egg Weight and Production. Age at sexual maturity was determined for each bird and was defined as the day of the first oviposition. BW and egg weight at sexual maturity was also recorded. All eggs were collected daily and weighed. A code was assigned to each egg based on its weight, shell quality, and the number of yolks. A defective egg was categorized as an egg with any one of the following: more than one yolk, a soft-shell, membranous shell, or an abnormal shell. A normal egg was one that had an intact shell and a single yolk. Eggs that were broken by the handler or pecked by the bird were also considered normal. A settable egg was defined as a normal egg that weighed over 52 g (considered minimum acceptable weight by Canadian hatcheries). The assignment of a code allowed for the calculation of weekly hen-day egg production, total, normal, and settable egg number. Differences in prime sequence length, average sequence length, sequence number, pause length, and the number of ovulations were analyzed using a software program, the Egg Production and Sequence Analyzer[2].

Every 28-d beginning at 31 wk of age, two normal eggs from each hen were opened to determine the weight of the egg components. Only eggs that had been laid over the previous three days were used in order to minimize differences in egg weight caused by storage. Specific gravity, post storage egg weight, and yolk weight were determined. The shells were rinsed with tap water, air-dried at room temperature for 4 d and then weighed. Differences in egg weight between when the egg was laid and when it was opened were assumed to be caused by albumen losses. Therefore, albumen weight was determined by substracting yolk and shell weights from the weight of the egg when it was laid.

Fertility and Hatchability. Once the flock had achieved 86% weekly egg production (31 wk of age), the hens were artificially inseminated with 50 µl of fresh pooled semen collected from caged broiler breeder roosters at 7-d intervals. Each day, after the eggs had been weighed, the settable eggs were placed in a cooler (60-65 F; 80% relative humidity) in lots based on the strain of the bird and the age at photostimulation. Eggs collected over a 7-d period were sent to a commercial hatchery[3] and incubated. At hatch, the number of chicks was counted and unhatched eggs were opened to determine fertilization and/or the stage of embryonic development. For the purposes of this trial, clear eggs were assumed to be infertile. Fertility was calculated within a lot as the number of fertile eggs per 100 eggs set in the incubator. Hatchability was calculated as the number of chicks hatched per 100 eggs set, and hatchability of fertile eggs was calculated as the number of chicks hatched per 100 fertile eggs set. Chick production was calculated by multiplying the number of fertile eggs by the hatchability of fertile eggs.

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[2] Version 3.00. Copyright © 1999. Alberta Agriculture, Food and Rural Development, #204, 7000-113 Street, Edmonton, AB, T6H 5T6, Canada.

[3] Lilydale Foods Co-operative Ltd., 7503-127 Avenue, Edmonton, AB, Canada, T5C 1R9

Carcass Parameters. Prior to processing, the shank and keel lengths were measured on each bird as an assessment of frame size. Using a vernier caliper, shank length was determined by measuring the length of the tibiotarsus (from the top of the hock joint to the footpad) and keel length was determined by measuring the distance from the hypocleidum-clavical joint to the caudal end of the sternum. A chest width measurement was taken on all of the A birds using vernier calipers placed under the birds wings, 2.5-cm below the clavicle bones and measured across the front of the body.

Birds were euthanatized by cervical dislocation and then weighed individually. The *Pectoralis major* and *Pectoralis minor*, liver, abdominal fat pad, ovary, and oviduct were removed from the carcass and individually weighed. Contents in the oviduct were removed before oviduct weight was determined. Differences in ovarian parameters were assessed by classifying follicles into categories depending on their size (Robinson and Etches, 1986) and counted. Follicles between 1 and 5 mm in diameter were designated white follicles (WF). The next category was follicles measuring between 5 and 10 mm in diameter, known as small yellow follicles (SYF). A follicle greater than 10 mm in diameter was classified as a large yellow follicle (LYF). Follicles in this category established the ovarian hierarchy, as they were all in the process of rapid follicular growth and maturation (Gilbert and Wells, 1984). Each LYF was individually weighed and the largest follicle was designated the first follicle to ovulate (F1) (Bahr and Johnson, 1984). The incidence of atretic WF, LYF, and SYF, characterized by a discolored and/or shrunken appearance, were also noted (Gilbert et al., 1983). A stroma weight was also determined by weighing the ovary after the LYF and atretic LYF had been removed.

For the A birds, a digital image of the *Pectoralis major* was taken with the software program Northern Exposure®.[4] The breast muscle was placed on a clean white surface and any peripheral fat and/or tissue was removed. An image was captured and then saved in black and white. Area and linear (length and width) measurements were then assessed from the digital image (Figure 3-1A). A 1-cm slice was made from the left side of the *Pectoralis major* beginning proximal to the wing attachment and continuing to the medial caudal point of the muscle (long slice). Another 1-cm slice was made from the right side of the *Pectoralis major* beginning at the widest point of the muscle and continuing across, staying perpendicular to the keel (short slice). Both the long and short slices were placed a white surface and a digital image was recorded. One length measurement and three width measurements were taken on each slice (Figure 3-1B). The purpose was to assess strain differences in breast fleshing, such as thickness and uniformity, as some strains were selected more for breast yield than others.

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[4] Northern Exposure, Empix Imaging Inc., Missisauga, ON, Canada, L5L 5M6

Statistical Analysis

Pullets within a strain were assigned to a cage and a treatment in a completely randomized design. The experiment was set up as a 3 × 2 factorial design with three strains and two ages at photostimulation as the main effects. The data (excluding sequence analysis) were analyzed by two-way analysis of variance using the GLM procedure of SAS® (SAS Institute, 1999). Sequence length parameters were analyzed as a three-way analysis of variance also using the GLM procedure of SAS® (SAS Institute, 1999) with strain, age at photostimulation, and age of bird as the main effects. The data were analyzed using repeated measures (split plot) analysis according to the procedure outlined by Goonewardene and Florence (1992). Strain, age at photostimulation, and strain × age at photostimulation were tested against the experimental unit cage(strain × age at photostimulation). Differences between means were determined using the pdiff option of the LSMEANS statement of SAS® (SAS Institute, 1999). The error variation for strain and age at photostimulation was the variation between birds. Two birds that had not laid an egg for 5 wk or more were removed from the trial. One bird was culled because of a sexing error and was also removed from the data set. The lack of sufficient calcium in the diet during the early lay period had no effect on mortality. The standard error of the mean (SEM) was determined by using the group with the least number of birds. Probability values in tables and figures were taken from the ANOVA table for each parameter.

3.3 RESULTS AND DISCUSSION

Carcass Characteristics before Photostimulation

Strain differences in carcass parameters were assessed before the treatments began (19 wk of age) and are presented in Table 3-3. There was no difference in BW at the time of processing. This was not suprising as all of the birds in this trial had been selected based on similar BW. The chest width measurement was higher for EXP pullets than Classic pullets. EXP pullets also had a higher breast weight at 19 wk of age than Classic pullets. This was caused by differences in *Pectoralis major* weight, not *Pectoralis minor* weight. As the EXP birds had been bred selectively for more breast yield than the Classic or FSY strains it is not suprising that they had a larger *Pectoralis major*. Interestingly, the FSY pullets, which were not selected for breast yield as much as the EXP line, was intermediate in breast weight between the Classic and EXP pullets.

Despite a higher chest width measurement for the EXP pullets, there was no difference in the width of the actual muscle (Table 3-4; whole breast image: width). Likewise, the measurement of area of the *Pectoralis major* was not different by strain. There were, however, differences in the width measurements of the long and short slices. The two slices of the *Pectoralis major* served as an indicator of muscle thickness. The center of the long slices measured 1.46 ± 0.04 cm wide (mean ± SEM) for the EXP pullets and 1.31 ± 0.04 cm wide for the Classic pullets. The top of the short slice was also wider for EXP than Classic pullets (1.95 ± 0.06 and 1.72 ± 0.06 cm, respectively). The bottom of the short slice was wider for EXP than FSY or Classic birds. These measurements reflect the middle region of the breast muscle, indicating that EXP birds have increased fleshing in this area, rather than at the cranial or caudal ends compared to the other strains.

Sexual Maturity Parameters

There was no strain difference in age at sexual maturity (Table 3-5). As expected, birds that were delayed in age at photostimulation were older at sexual maturity (180.0 ± 1.1 and 185.6 ± 1.1 d of age, for 20-wk and 23-wk treatments, respectively). However once photostimulated, the pullets in the 23-wk treatment took approximately 15 d less to lay their first egg than the pullets in the 20-wk treatment. The weight of the first egg was greater for the 23-wk treatment than the 20-wk treatment. The later-photostimulated pullets also weighed more at first oviposition than the early-photostimulated pullets agreeing with observations made by Yuan et al. (1994) and Robinson et al. (1996). Increased age at photostimulation was related to increased BW at sexual maturity. This may have been caused by an increase in body fat. Brody et al. (1984) noted that birds photostimulated at an older age had larger abdominal fat pads. Leeson et al. (1988) also noted that carcass fat increased and carcass protein decreased with delayed photostimulation. Strain and age of pullet at photostimulation did not affect shank and keel lengths at first oviposition. Robinson et al. (1996) observed that delaying photostimulation allowed pullets to obtain a more mature frame size. Although there were no differences in shank and keel lengths observed in the present study, the higher BW of the hens in the 23-wk treatment lends support to this view.

Egg Parameters

Egg Weight. Strain and treatment effects on egg weight are presented in Table 3-6. Egg weight throughout lay was not affected by genotype. Age at photostimulation, did affect egg size in the early lay period. The later-photostimulated hens laid heavier eggs than the early-photostimulated hens when 25 to 34 wk of age. This coincided with a heavier BW from 27 to 34 wk of age in the 23-wk group, agreeing with McDaniel et al. (1981) who found that BW was positively correlated with egg weight. Yuan et al. (1994) did not find any effect of treatment on egg weight despite noting an increase in BW in response to delayed photostimulation. Differences in egg size continued throughout the laying cycle even though BW was no longer different among the treatments during the late laying period. Mean weekly egg weights for each treatment are presented in Figure 3-2.

Egg Components. Throughout lay, egg components were assessed (Tables 3-7 and 3-8). Overall, the Classic strain had proportionately more shell than the other strains, with mean egg weight remaining the same for all three strains. The difference in egg weight, related to age at photostimulation, was mainly a result of proportionately greater albumen content in the egg for the birds photostimulated at 23 wk of age. Eggs from Classic birds and the 20-wk treatment also had a higher specific gravity than their strain or treatment counterparts, indicating a higher shell quality. This was probably a result of a thicker shell as Frank et al. (1964) found that specific gravity was a good measure of shell thickness and Joseph et al. (1999) observed a strong positive correlation between shell weight and specific gravity. There were some differences in yolk weight, however they were not consistent across strains or treatments.

Egg Production Parameters

Hen-Day Egg Production. There was no strain difference in weekly percent hen-day egg production during the early lay period of 25 to 34 wk of age (Table 3-9). Peak egg production was also not affected by strain (92.3 ± 2.4, 87.5 ± 2.5, and 86.3 ± 2.5% for Classic, FSY, and EXP, respectively). However from 35 to 44 wk of age EXP hens had a lower rate of egg production (75.7 ± 1.4%) compared to Classic and FSY hens (80.3 ± 1.4 and 80.3 ± 1.4%, respectively). Analysis of normal egg number during this mid-lay period showed that the Classic and FSY strains produced three more eggs per hen compared to the EXP strain (54.7 ± 0.9, 54.3 ± 0.9, 51.3 ± 0.9 normal eggs, for Classic, FSY and EXP strains, respectively). Unfortunately, the additional eggs were considered unsettable (less than 52 g). Differences in egg production were not related to differences in BW across strains and it did not carry over into the late lay period.

During the early lay period (25 to 34 wk of age) the 20-wk treatment had a higher rate of egg production (78.6 ± 1.7%) than the 23-wk treatment (73.2 ± 1.7%). This difference of 5.4% was attributable to the earlier age at sexual maturity for the 20-wk treatment and resulted in the production of an additional five eggs per hen. Although these eggs had single yolks and intact shells, they weighed less than the 52 g threshold and were therefore unsettable. Peak egg production was achieved by 31 wk of age for both treatments and was not significantly different (87.7 ± 2.0 and 87.9 ± 2.0%, for birds photostimulated at 20 and 23 wk of age, respectively). This is in contrast to the results of Yuan et al. (1994) who found that delaying photostimulation to 20 wk of age resulted in a higher peak egg production than photostimulating at 14 or 17 wk of age. By the mid-lay period in the present study, there was no difference in egg production between the two treatments. Overall, there were no differences in hen-day egg production (75.0 ± 1.1 and 73.4 ± 1.1%, for 20- and 23-wk treatments, respectively). Weekly egg production for strain and age at photostimulation are presented in Figures 3-3 and 3-4, respectively.

Egg Numbers. As there was no effect of strain or age at photostimulation on overall hen-day egg production, the lack of difference in total, normal, or settable egg numbers was not suprising (Table 3-10). Therefore, although delaying photostimulation resulted in the production of larger eggs throughout the trial, it did not result in an increase in the number of settable eggs produced. The interaction of strain and age at photostimulation also had no effect on egg numbers. Therefore EXP hens produced as many eggs as the Classic and FSY hens. This result was unexpected as both the FSY and EXP hens have been selected for more breast yield than the Classic hens and selection for growth rate is usually negatively correlated with reproductive efficiency (Siegel and Dunnington, 1985). Harrison et al. (1969) noted that although postponing photostimulation delayed sexual maturity, there was no effect on egg production of commercial egg-laying stocks. Likewise, delaying sexual maturity for broiler breeders had no effect on total egg production or egg number (Yuan et al., 1994; Robinson et al., 1996). The results from the present study are positive as it indicates that delaying age at photostimulation does not shorten the production cycle, as there was no decrease in the number of eggs produced.

Sequence Length Analysis. Although there were no strain differences in egg numbers, there was a strain effect on prime sequence length (Table 3-11). The Classic birds had longer prime sequences than the EXP birds (23.8 ± 1.8 and 17.6 ± 1.8 d, respectively). As with breast muscle weight, the mean prime sequence length of the FSY birds was intermediate between the Classic and EXP strains (20.4 ± 1.8 d). Average sequence length was not affected by strain but EXP birds had a longer pause between sequences than Classic or FSY birds. Jaap and Muir (1968) found that meat-type hens had an increased incidence of erratic oviposition timing, resulting in arrhythmic sequences, compared to an unselected meat-type line and an egg-type line of hens. Robinson et al. (1991) found that full-fed hens laid shorter prime sequences than restricted-fed breeders. As well, feed restricted hens, that represented the upper 50% of the flock in terms of egg production, had long prime sequences and shorter pause lengths compared to hens in the lower 50% of the flock (Robinson et al. 1990). It is possible that the EXP line may need to be reared at a heavier BW than the FSY line, as they have been further selected for growth rate. If this is true, then the EXP line in the present study weighed less than their optimal BW at sexual maturity and were not physiologically prepared for egg production. This could explain why the EXP strain laid a shorter prime sequence and had longer intersequence pauses than the Classic strain.

Fertility and Hatchability. Fertility and hatchability data are presented in Table 3-12. Birds photostimulated at 23 wk of age had a lower rate of fertility (89.4 ± 0.8%) than birds photostimulated at 20 wk of age (92.0 ± 0.8%). There is no explanation for this difference as age at photostimulation has not been shown to affect the fertility of eggs. Despite this difference, there was no effect of strain or treatment on hatchability of eggs set or hatchability of fertile eggs. Robinson et al. (1996) also noted that age at photostimulation had no effect on the hatchability of eggs. However, broiler breeders photostimulated at older ages produced more chicks per hen compared to those photostimulated at younger ages (Robinson et al., 1996). In the present study, there were no strain or treatment influences on chick production. The number of chicks produced per hen was 114.4 ± 3.8, 109.8 ± 3.8, and 108.2 ± 3.8, for Classic, FSY, and EXP strains, respectively. Hens photostimulated at 20 wk of age produced 113.2 ± 3.1 chicks per hen compared to 108.9 ± 3.1 chicks per hen for birds photostimulated at 23 wk of age. The results from this study agree with those of Robinson et al. (1996) in that differences in chick production only occurred between pullets photostimulated at 130 d (18.5 wk) versus 140 d (20 wk) of age. There were no differences in chick production between pullets photostimulated at 140 d (20 wk), 150 d (21.5 wk), or 160 d (23 wk) of age. The interaction of strain and age at photostimulation did not yield any significant differences.

Carcass Characteristics at the End of Lay

Differences in carcass parameters at 53 wk of age were mainly the result of strain influences (Table 3-13). Processing BW, although not different, at the onset of the trial, was different at 53 wk of age. EXP hens weighed more than Classic hens. This was expected as live BW was different for the three strains from 50 to 53 wk of age. Breast weight, which included both the *Pectoralis major* and *Pectoralis minor* was significantly higher for EXP than Classic or FSY. Again, this was largely attributed to differences in the *Pectoralis major* weight, although the weight of the *Pectoralis minor* was also affected by the strain of the hen. Thus, the EXP strain had a higher breast muscle weight at photostimulation that remained higher at the end of lay.

Both strain and treatment affected liver weight. Classic hens had a lower liver weight compared to FSY and EXP hens. Hens on the 23-wk treatment also had a lower liver weight than the hens on 20-wk treatment. Abdominal fat pad weight was not proportionately different among strains or treatments. Although the strain of hen affected BW and breast muscle weight, there were no effects of strain on the weight of the reproductive organs (Table 3-14). The age at which the birds were photostimulated affected ovary weight, with the 23-wk treatment having a higher ovary weight than the 20-wk treatment. Although egg weight was consistently higher for the 23-wk treatment, it was primarily because of increased albumen weight, there were no differences in yolk weight on either an absolute or relative basis. The number of LYF in the hens from 23-wk treatment was significantly higher (5.49 ± 0.12 LYF) than in the hens from 20-wk treatment (5.10 ± 0.12 LYF; Table 3-15). This contributed to the larger ovary weight in the 23-wk treatment. It would seem that delaying photostimulation had a positive impact, increasing the number of LYF at the end of the egg production cycle. This may explain why these birds were able to produce as many eggs as the early photostimulated birds, despite the delay in sexual maturity. Robinson et al. (1996) found that ovary weight and the number of LYF at 60 wk of age were not affected by age at photostimulation. Showed some interaction with age at photostimulation. The hens of the Classic strain had a higher ovary weight when photostimulated at 23 wk than at 20 wk of age. The same was true for the EXP hens and the difference was greater. This suggests that delaying photostimulation allowed the pullets more time to complete their growth so that once photostimulated, more nutrients were allocated to egg production.

It is estimated that the first 4 to 8 eggs laid by a broiler breeder hen are unsettable as they are below the 52 g threshold (F. E. Robinson, personal communication). As such, the production of small eggs is a leading issue for hatching egg producers. Delaying photostimulation from 20 to 23 wk of age in this trial delayed sexual maturity by only 6 d. This did not translate into differences in settable egg number, but it did increase egg size early in lay, a difference that remained until the termination of the experiment. The effects of delaying photostimulation on egg weight were attributed to an increase in BW in this treatment. Presumably, this treatment allowed the broiler breeder more time to complete skeletal and muscle growth. Robinson et al. (1996) noted that head width, keel length, and girth all increased as age at photostimulation increased. At 23 wk of age then, the broiler breeder pullets in the present trial had probably begun partitioning a greater proportion of their energy intake into fat deposition and reproductive organ development. Therefore, when photostimulated, they were able to respond more quickly taking only 24.6 d to reach sexual maturity as opposed to 40.0 d in the 20-wk treatment. This supports our first hypothesis, in that the rate of sexual maturation was higher for the pullets photostimulated at 23 wk of age. Although there were differences among strains in breast muscle weight, selection for breast yield did not affect the number of eggs produced. All three strains responded similarly to the different ages at photostimulation, with the exception of ovary weight, which increased for both the Classic and EXP hens in response to delayed photostimulation. The increase in ovary weight was greater for the EXP hens than Classic hens. Perhaps, as hypothesized, the EXP hens are slower to sexually mature, as they need to be reared at a heavier BW.This supports our second hypothesis that delaying photostimulation gave the EXP hens more time to physiologically prepare for egg production.

Table 3-1. The composition and nutrient intake of the starter and grower diets given to female broiler breeder pullets during the rearing period (0 to 19 wk of age)

Ingredient	Starter diet 0 to 6 wk of age	Grower diet 6 to 19 wk of age
	%	%
Wheat, hard red winter	44.23	34.42
Ground corn	14.14	16.44
Soybean meal (44% CP)	17.34	7.37
Wheat shorts	7.50	15.00
Oats	5.00	12.50
Barley	5.00	10.00
Tallow	2.00	0.07
Ground limestone	1.65	1.72
Biofos	1.58	0.86
Choline chloride premix[1]	0.50	0.50
Broiler Premix[2]	0.50	0.50
Salt	0.38	0.33
D, L-methionine	0.14	0.13
L-Lysine	0.03	0.16
Monensin	0.08	0.05
Nutrient composition		
CP (analyzed), %	18.1	14.6
ME (calculated), kcal per kg	2783	2711
Calcium (analyzed), %	1.00	0.98
Available phosphorus (calculated),	0.47	0.32
Methionine (calculated), %	0.41	0.34
Lysine (calculated), %	0.84	0.72

[1] Choline chloride premix supplied at a level of 100 mg per kilogram of diet.

[2] Broiler premix supplied the following per kilogram of diet: vitamin A, 10,000 IU; vitamin D3, 2,500 IU; vitamin E, 35 IU; vitamin K, 2.0 mg; pantothenic acid, 14 mg; riboflavin 5.0 mg; folacin, 0.8 mg; niacin, 65 mg; thiamine, 2.0 mg; pyridoxine, 4.0 mg; vitamin B_{12}, 0.015 mg; biotin, 0.18 mg; iodine, 0.5 mg; Mn, 70.0 mg; Cu, 8.5 mg; Zn, 80.0 mg; Se, 0.1 mg; Fe, 100.0 mg.

Table 3-2. The composition and nutrient intake of the pre-breeder and breeder diets given to the female broiler breeders during the trial period (19 to 53 wk of age)

Ingredient	Pre-breeder diet 19 to 31 wk of age	Breeder diet 31 to 53 wk of age
	%	%
Wheat, hard red winter	24.10	22.01
Ground corn	30.00	34.24
Soybean meal (48% CP)	13.19	13.31
Oat groats	15.00	17.20
Oats	3.35	---
Barley	8.26	---
Corn gluten meal	---	1.47
Canola oil	0.90	1.91
Ground limestone	1.95	6.54
Dicalcium phosphate	1.76	1.81
Choline chloride premix[1]	0.50	0.50
Layer premix[2]	0.50	0.50
Salt	0.35	0.36
D, L-methionine	0.08	0.07
L-Lysine	0.07	0.09
Nutrient composition		
CP (analyzed), %	16.5	16.1
ME (calculated), kcal per kg	2900	2900
Calcium (analyzed), %	1.34	2.95
Available phosphorus (calculated),	0.45	0.45
Methionine (calculated), %	0.32	0.32
Lysine (calculated), %	0.74	0.74

[1] Choline chloride premix supplied at a level of 100 mg per kilogram of diet.

[2] Layer premix supplied the following per kilogram of diet: vitamin A, 12,000 IU; vitamin D3, 3,000 IU; vitamin E, 40 IU; vitamin K, 2.0 mg; pantothenic acid, 14.0 mg; riboflavin 6.5 mg; folacin, 1.0 mg; niacin, 40 mg; thiamine, 3.3 mg; pyridoxine, 6.0 mg; vitamin B_{12}, 0.02 mg; biotin, 0.2 mg; iodine, 0.5 mg; Mn, 75.0 mg; Cu, 15.0 mg; Zn, 80.0 mg; Se, 0.1 mg; Fe, 100.0 mg.

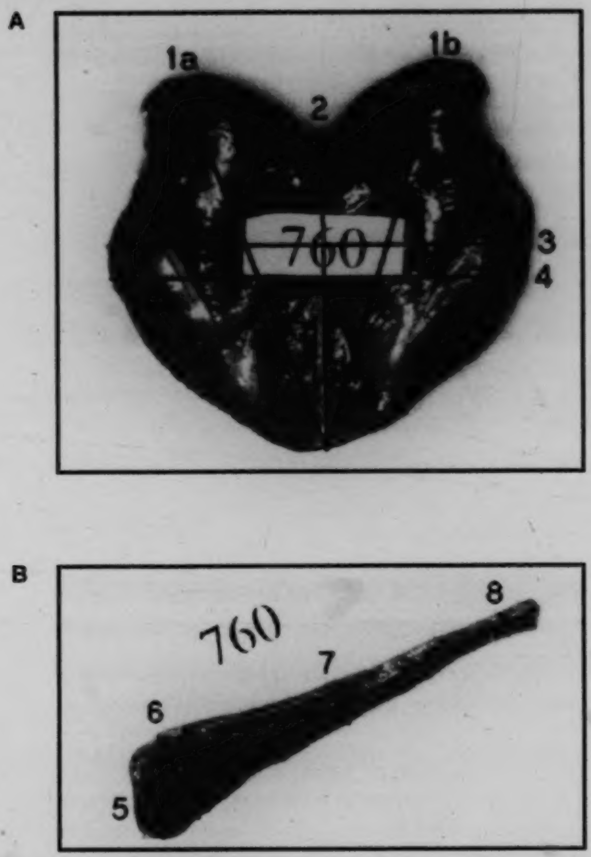

Figure 3-1. A: Digital image of a *Pectoralis major* taken from a broiler using image analysis. Linear measurements (cm) were made on each image of a female broiler breeder breast muscle, 1a and b: Length from left and right side, respectively, 2: Length from center, 3: Width (not measured for this study), 4: Width taken at the widest point across the muscle. B:Digital image of the long slice of a Pectoralis major taken from a broiler using image analysis. Using a double-bladed scalpel a 1-cm transverse section was made from the left side of the *Pectoralis major* beginning proximal to the wing attachment and continuing to the medial caudal point of the muscle. Linear measurements (cm) were made on the long slice, 5: Length, 6: Top width, 7: Center width, 8: Bottom width. The short slice (picture not shown) was a transverse section taken from the right side of the *Pectoralis major* beginning proximal to the keel attachment and continuing right to the end of the muscle. Measurements on the short slice were similar to that of the long slice.

Table 3-3. Carcass characteristics measured at 19 wk of age, one wk prior to onset of treatments from three strains of broiler breeder pullets

	Strain			
Parameter	Classic	FSY[1]	EXP[2]	SEM
n	37	38	38	---
Carcass characteristics				
BW at processing (kg)	1.882	1.862	1.893	0.059
Shank length (mm)	104.4	104.2	104.5	0.7
Keel length (mm)	141.0	140.9	143.1	1.8
Chest width[3] measurement (mm)	65.1^{b}	68.1^{ab}	69.3^{a}	1.3
Breast muscle parameters				
Breast weight[4] (%)	15.13^{b}	15.76^{ab}	16.23^{a}	0.23
Pectoralis major weight (%)	11.12^{b}	11.71^{ab}	12.04^{a}	0.19
Pectoralis minor weight (%)	4.00	4.05	4.19	0.06
Liver weight (%)	2.20	2.23	2.17	0.04
Abdominal fat pad weight (%)	1.01	0.87	0.82	0.12
Reproductive characteristics				
Oviduct weight (g)	0.35	0.36	0.38	0.04
Ovary weight (g)	0.50	0.48	0.49	0.02
Atretic WF(no.)	0.38	0.13	0.37	0.09

[1] FSY: Arbor Acres Feather Sexable Yield.

[2] EXP: Arbor Acres experimental line selected for increased breast muscle yield.

[3] Chest width: measurement taken across the chest of the bird, one inch below the clavicle bones.

[4] Breast weight: *Pectoralis major* and *Pectoralis minor* weight.

[5] Atretic WF: atretic white follicles; follicles between 1 and 5 mm in diameter, characterized by a shrunken and/or discolored appearance.

[a,b] Means within a row with no common superscript differ significantly ($P \leq 0.05$).

Table 3-4. Measurements taken of the *Pectoralis major*, using digital image analysis,[1] from three strains of broiler breeder pullets processed at 19 wk of age

	Strain			
Parameter	Classic	FSY[2]	EXP[3]	SEM
Whole breast image				
Length from left side (cm)	17.97	18.07	17.58	0.22
Length from right side (cm)	17.99	18.03	17.65	0.22
Length from center (cm)	13.25^{ab}	13.50^{a}	12.77^{b}	0.21
Width[4] (cm)	17.25	17.28	17.26	0.28
Area (cm^2)	209.13	205.29	208.28	5.25
Long slice[5] image				
Length (cm)	20.92	21.03	20.72	0.26
Width, top (cm)	2.06	2.16	2.09	0.07
Width, center (cm)	1.31^{b}	1.39^{ab}	1.46^{a}	0.04
Width, bottom (cm)	0.80	0.78	0.75	0.03
Short slice[6] image				
Length (cm)	10.04	9.97	10.13	0.18
Width, top (cm)	1.72^{b}	1.78^{ab}	1.95^{a}	0.06
Width, center (cm)	1.27	1.40	1.37	0.05
Width, bottom (cm)	1.52^{b}	1.54^{b}	1.69^{a}	0.05

[1] Digital image analysis: using the software program Northern Exposure® by Empix Imaging Inc., Mississauga, ON, Canada, L5L 5M6.

[2] FSY: Arbor Acres Feather Sexable Yield.

[3] EXP: Arbor Acres experimental line selected for increased breast muscle yield.

[4] Width: the width measurement was taken across the *Pectoralis major* at the widest point.

[5] Long slice: transverse section of the *Pectoralis major* taken from the left side of the muscle beginning proximal to the wing attachment and continuing downwards to the medial caudal point of the muscle.

[6] Short slice: transverse section of the *Pectoralis major* taken from the right side of the muscle beginning proximal to the keel attachment and continuing right to the end of the muscle.

[a,b] Means within a row with no common superscript differ significantly ($P \leq 0.05$).

Table 3-5. Differences in age, BW, and egg weight at sexual maturity (SM) for three strains of female broiler breeders photostimulated at either 20 or 23 wk of age

	Parameters measured					
Source	Age at SM[1]	Days from PS[2] to SM[1]	BW	Egg weight[3]	Shank length	Keel length
	d	d	kg	g	mm	mm
Strain						
Classic	183.1	32.6	3.228	44.8	107.4	153.6
FSY[4]	183.7	33.2	3.208	45.3	108.7	157.0
EXP[5]	181.6	31.1	3.196	45.9	107.9	154.9
SEM	1.3	1.3	0.043	0.8	0.9	1.3
Age at photostimulation						
20 wk	180.0^{b}	40.0^{a}	3.136^{b}	44.4^{b}	107.8	155.8
23 wk	185.6^{a}	24.6^{b}	3.285^{a}	46.3^{a}	108.2	154.5
SEM	1.1	1.1	0.034	0.7	0.7	1.1
	----------Probability----------					
Source of variation						
Strain	0.484	0.484	0.868	0.645	0.518	0.142
Age at photostimulation	0.0002	0.0001	0.003	0.041	0.702	0.365
Interaction	0.202	0.202	0.138	0.128	0.522	0.753

[1] SM: sexual maturity; defined as first oviposition.

[2] PS: photostimulation.

[3] Egg weight: only eggs with a single yolk and a hard, intact shell were used to calculate egg weight.

[4] FSY: Arbor Acres Feather Sexable Yield.

[5] EXP: Arbor Acres experimental line selected for high breast muscle yield.

^{a,b}Means within a row with no common superscript differ significantly ($P \leq 0.05$).

Table 3-6. Mean egg weight, during the early, mid, and late lay periods, from three strains of broiler breeders, photostimulated at either 20 or 23 wk of age

	Egg weight[1]			
Source	Early lay period (25 to 34 wk of age)	Mid lay period (35 to 44 wk of age)	Late lay period (45 to 53 wk of age)	Overall (25 to 53 wk of age)
	g	g	g	g
Strain				
Classic	57.2	63.2	65.1	61.3
FSY[2]	57.5	63.3	65.9	61.9
EXP[3]	57.3	63.2	65.4	61.5
SEM	0.6	0.6	0.7	0.1
Age at photostimulation				
20 wk	56.6^{b}	62.4^{b}	64.6^{b}	60.8^{b}
23 wk	58.1^{a}	64.0^{a}	66.3^{a}	62.3^{a}
SEM	0.5	0.5	0.6	0.1
	---------- Probability ----------			
Source of variation				
Strain	0.913	0.995	0.639	0.780
Age at photostimulation	0.026	0.017	0.014	0.018
Interaction	0.182	0.218	0.244	0.172

[1] Egg weight: only eggs with a single yolk and a hard, intact shell were used to determine mean egg weight.

[2] FSY: Arbor Acres Feather Sexable Yield.

[3] EXP: Arbor Acres experimental line selected for high breast muscle yield.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

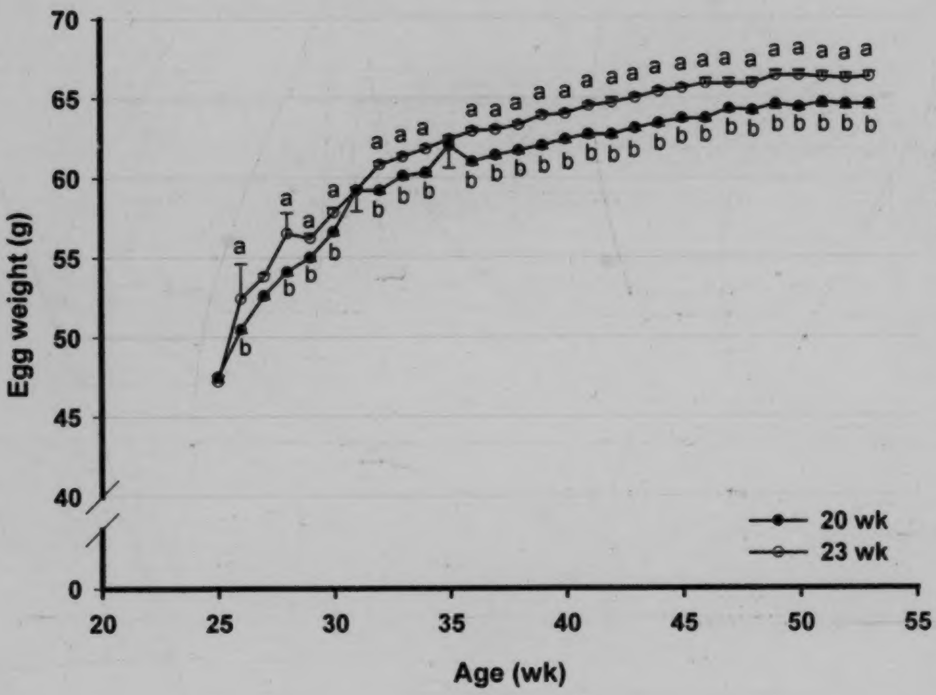

Figure 3-2. Mean (± SEM) weekly egg weight, from 25 to 53 wk of age, from broiler breeders photostimulated at either 20 or 23 wk of age. ^{a,b} Means within an age with no common superscript differ significantly ($P \leq 0.05$).

Table 3-7. Egg traits measured at 31, 35, and 39 wk of age from three strains of broiler breeders photostimulated at either 20 or 23 wk of age

	Strain				Age at photostimulation		
Parameter	Classic	FSY[1]	EXP[2]	SEM	20 wk	23 wk	SEM
Age: 31 wk							
Egg weight (g)	58.3	58.4	57.9	0.6	57.3^b	59.1^a	0.5
Yolk weight (%)	27.8	27.7	28.1	0.3	28.3^a	27.5^b	0.2
Albumen weight (%)	62.9	63.7	63.2	0.3	62.7^b	63.8^a	0.3
Shell weight (%)	9.28^a	8.67^b	8.71^b	0.11	9.07^a	8.70^b	0.09
Age: 35 wk							
Egg weight (g)	60.9	61.6	61.1	0.6	60.4^b	62.0^a	0.5
Yolk weight (%)	29.0	29.1	29.5	0.3	29.5	28.9	0.2
Albumen weight (%)	62.1	62.9	62.3	0.3	62.0^b	62.9^a	0.3
Shell weight (%)	8.88^a	8.09^b	8.27^b	0.10	8.57^a	8.26^b	0.08
Specific gravity	1.0760^a	1.0715^b	1.0721^b	0.0007	1.0741^a	1.0722^b	0.0005
Age: 39 wk							
Egg weight (g)	62.4	63.0	62.8	0.6	61.9^b	63.5^a	0.5
Yolk weight (%)	29.6^b	30.1^{ab}	30.5^a	0.3	30.4	29.8	0.2
Albumen weight (%)	61.5	61.8	61.2	0.3	61.0^b	62.0^a	0.3
Shell weight (%)	8.90^a	8.15^b	8.30^b	0.09	8.65^a	8.25^b	0.07
Specific gravity	1.0757^a	1.0721^b	1.0720^b	0.0006	1.0742^a	1.0723^b	0.0004

[1] FSY: Arbor Acres Feather Sexable Yield.

[2] EXP: Arbor Acres experimental line selected for high breast muscle yield.

[a,b] Means within a row and within an age group with no common superscript differ significantly ($P \leq 0.05$).

Table 3-8. **Egg traits measured 43, 47, and 51 wk of age from three strains of broiler breeders photostimulated at either 20 or 23 wk of age**

	Strain				Age at photostimulation		
Parameter	Classic	FSY[1]	EXP[2]	SEM	20 wk	23 wk	SEM
Age: 43 wk							
Egg weight (g)	64.2	63.8	64.0	0.7	63.1	64.9	0.6
Yolk weight (%)	29.9	30.6	30.9	0.3	30.8	30.2	0.3
Albumen weight (%)	61.0	60.7	61.1	0.3	60.5^{b}	61.4^{a}	0.3
Shell weight (%)	9.06^{a}	8.23^{b}	8.41^{b}	0.09	8.70^{a}	8.43^{b}	0.07
Specific gravity	1.0787^{a}	1.0735^{b}	1.0737^{b}	0.0007	1.0757	1.0749	0.0005
Age: 47 wk							
Egg weight (g)	64.9	64.9	65.1	0.7	63.7^{a}	66.3^{b}	0.6
Yolk weight (%)	30.3	30.9	31.3	0.3	31.2^{a}	30.4^{b}	0.3
Albumen weight (%)	60.8	61.0	60.4	0.3	60.2^{b}	61.2^{a}	0.3
Shell weight (%)	9.02^{a}	8.40^{c}	8.13^{b}	0.10	8.65^{a}	8.38^{b}	0.08
Specific gravity	1.0764^{a}	1.0715^{b}	1.0724^{b}	0.0007	1.0739	1.0729	0.0005
Age: 51 wk							
Egg weight (g)	64.8	66.4	65.6	0.7	64.7^{b}	66.5^{a}	0.6
Yolk weight (%)	30.4^{b}	31.4^{a}	31.6^{a}	0.4	31.4	30.9	0.3
Albumen weight (%)	60.9	60.5	60.1	0.4	60.0^{b}	60.9^{a}	0.3
Shell weight (%)	8.81^{a}	8.11^{b}	8.31^{b}	0.10	8.62^{a}	8.21^{b}	0.08
Specific gravity	1.0764^{a}	1.0719^{b}	1.0723^{b}	0.0007	1.0750^{a}	1.0720^{b}	0.0006

[1] FSY: Arbor Acres Feather Sexable Yield.

[2] EXP: Arbor Acres experimental line selected for high breast muscle yield.

^{a,b}Means within a row and within an age group with no common superscript differ significantly ($P \leq 0.05$).

Table 3-9. Weekly hen-day egg production during the early, mid, and late laying periods for three strains female broiler breeders photostimulated at either 20 or 23 wk of age

	Hen-day egg production[1]			
Source	Early lay period (25 to 34 wk of age)	Mid lay period (35 to 44 wk of age)	Late lay period (45 to 53 wk of age)	Overall (25 to 53 wk of age)
	%	%	%	%
Strain				
Classic	77.4	80.3^{a}	69.0	75.8
FSY[2]	74.6	80.3^{a}	68.4	74.7
EXP[3]	75.7	75.7^{b}	64.1	72.1
SEM	2.1	1.4	1.8	1.4
Age at photostimulation				
20 wk	78.6^{a}	78.2	67.4	75.0
23 wk	73.2^{b}	79.3	67.0	73.4
SEM	1.7	1.1	1.5	1.1
	Probability			
Source of variation				
Strain	0.609	0.024	0.123	0.155
Age at photostimulation	0.024	0.465	0.876	0.330
Interaction	0.152	0.825	0.467	0.377

[1] Egg production: all eggs, including defective eggs, were used in the calculation of hen day egg production.

[2] FSY: Arbor Acres Feather Sexable Yield.

[3] EXP: Arbor Acres experimental line selected for high breast muscle yield.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

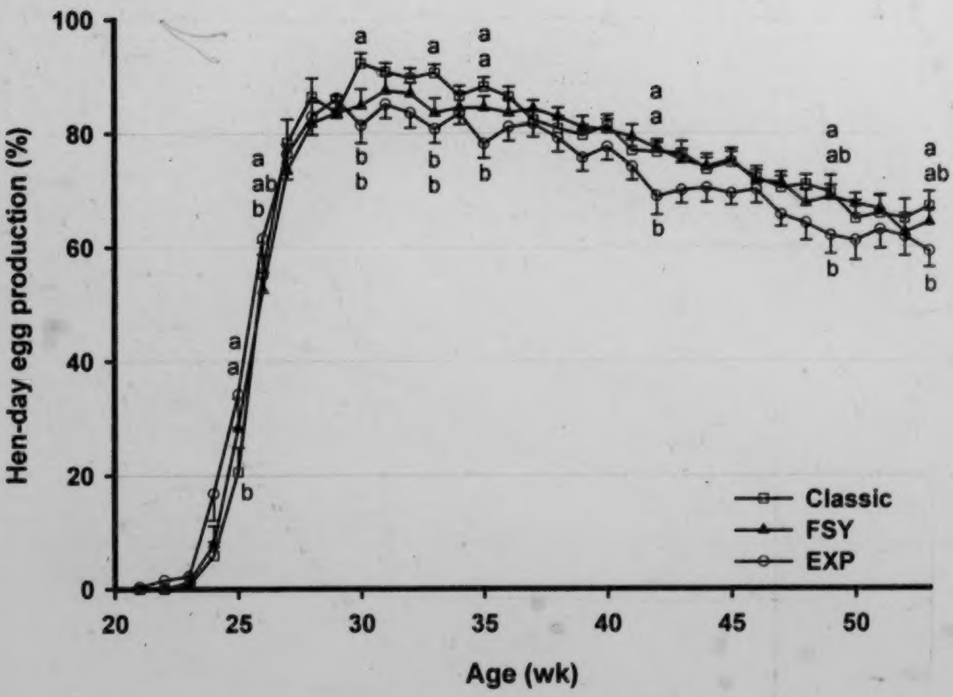

Figure 3-3. Mean (± SEM) weekly hen-day egg production, from 21 to 53 wk of age, of commercial broiler breeder females of three strains: Classic, FSY (Arbor Acres Feather Sexable Yield), and EXP (Arbor Acres experimental line). The number of weeks that Classic, FSY, and EXP hens were over 80% egg production was 12, 13, and 9 wk, respectively. ^{a,b} Means within an age with no common superscript differ significantly ($P \leq 0.05$).

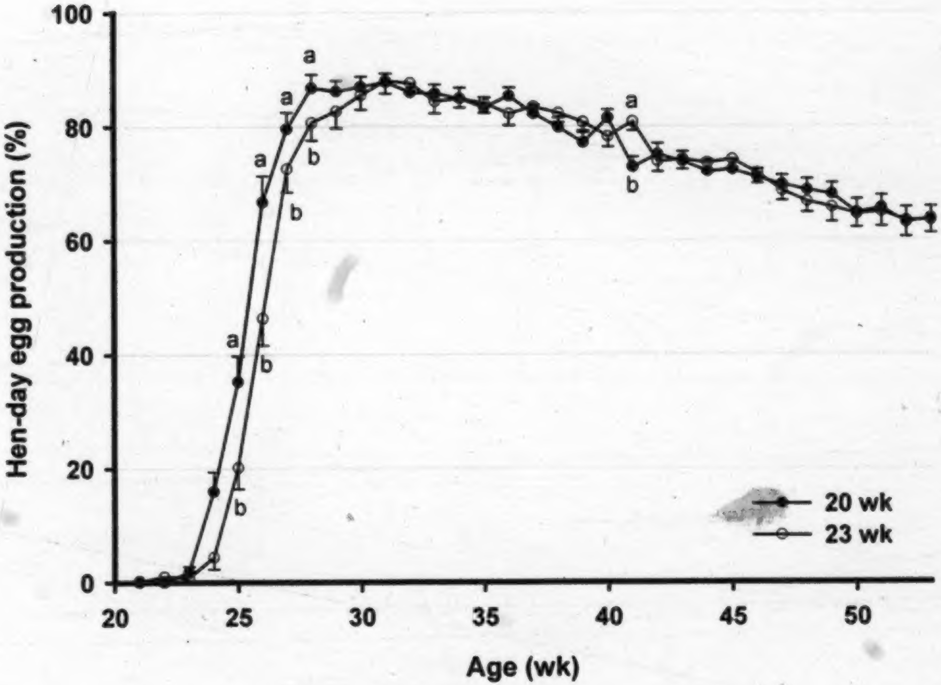

Figure 3-4. Mean (± SEM) weekly hen-day egg production, from 21 to 53 wk of age, of female broiler breeders, photostimulated at either 20 or 23 wk of age. The number of weeks that the 20- and 23-wk treatments were over 80% egg production was 11 and 13 wk, respectively). ^{a,b} Means within an age with no common superscript differ significantly (*P* ≤ 0.05).

Table 3-10. Cumulative total egg number, normal egg number, settable egg number, and number of ovulations per hen from 23 to 53 wk of age

	Egg parameters			
Source	Total egg Number[1]	Normal egg number[2]	Settable egg number[3]	Number of ovulations[4]
	#	#	#	#
Strain				
Classic	154.4	149.6	138.2	154.7
FSY[5]	152.3	146.1	133.9	152.9
EXP[6]	147.9	141.2	130.0	149.2
SEM	2.9	2.9	2.9	2.9
Age at photostimulation				
20 wk	153.5	148.6	134.5	154.2
23 wk	149.5	142.6	133.7	150.3
SEM	2.3	2.3	2.3	2.3
	------------Probability------------			
Source of variation				
Strain	0.261	0.115	0.144	0.381
Age at photostimulation	0.226	0.069	0.814	0.239
Interaction	0.389	0.310	0.663	0.449

[1] Total egg number: calculated by counting the number of eggs laid per hen (included both defective and normal eggs).

[2] Normal egg number: calculated by counting the number of eggs with a single yolk and hard, intact shell.

[3] Settable egg number: calculated by counting the number of eggs with a single yolk and a hard intact shell, weighing over 52.0 g. Eggs with a hard shell but broken were not included in the analysis.

[4] Number of ovulations: calculated by counting the number of yolks in both defective and normal eggs laid (i.e. a double yolk egg counted as one defective egg but two ovulations).

[5] FSY: Arbor Acres Feather Sexable Yield.

[6] EXP: Arbor Acres experimental line selected for high breast muscle yield.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

Table 3-11. Sequence parameters measured on three strains of broiler breeders, photostimulated at either 20 or 23 wk of age

	Sequence parameters measured			
Source	Prime sequence length[1]	Average sequence length	Number of sequences	Average pause length
	d	d	#	d
Strain				
Classic	23.8^{a}	4.59	36.9	1.17^{b}
FSY[2]	20.4^{ab}	4.46	38.1	1.19^{b}
EXP[3]	17.6^{b}	3.90	40.0	1.29^{a}
SEM	1.8	0.28	1.5	0.04
Age at photostimulation				
20 wk	20.7	4.34	39.4	1.19
23 wk	20.4	4.29	37.3	1.24
SEM	1.4	0.22	1.2	0.03
	--------------------------------Probability--------------------------------			
Source of variation				
Strain	0.046	0.169	0.337	0.045
Age at photostimulation	0.883	0.873	0.217	0.288
Interaction	0.588	0.666	0.430	0.825

[1] Prime sequence length: longest sequence of eggs laid; typically laid early in lay, therefore only strain data are presented.

[2] FSY: Arbor Acres Feather Sexable Yield.

[3] EXP: Arbor Acres experimental line selected for high breast muscle yield.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

Table 3-12. Fertility, hatchability of fertile eggs, and hatchability of settable eggs measured from 31 to 53 wk of age on three strains of broiler breeders, photostimulated at either 20 or 23 wk of age

	Hatchability parameters[1]		
Source	Fertility	Hatchability of fertile	Hatchability of eggs set
	%	%	%
Strain			
Classic	90.4	90.9	82.7
FSY[2]	89.8	89.1	81.2
EXP[3]	91.9	89.4	82.6
SEM	1.0	1.4	1.8
Age at photostimulation			
20 wk	92.0^a	91.1	84.0
23 wk	89.4^b	88.4	80.3
SEM	0.8	1.2	1.4
	-----------------------------------	---Probability---	-----------------------------------
Source of variation			
Strain	0.343	0.620	0.794
Age at photostimulation	0.027	0.105	0.060
Interaction	0.315	0.077	0.168

[1] Hatchability parameters: assessed by counting the number of live chicks hatched and by breaking open the hatch residue.

[2] FSY: Arbor Acres Feather Sexable Yield.

[3] EXP: Arbor Acres experimental line selected for high breast muscle yield.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

Table 3-13. Carcass parameters measured at 53 wk of age on three strains of broiler breeders, photostimulated at either 20 or 23 wk of age

Source	n	BW at processing	Shank length	Keel length	Breast weight[1]	*Pectoralis major* weight	*Pectoralis minor* weight	Liver weight	Abdominal fat pad weight
		Carcass parameters							
		kg	mm	mm	%	%	%	%	%
Strain									
Classic	48	3.762^b	110.2	153.3^c	15.25^b	11.57^b	3.68^b	1.37^b	4.83
FSY[2]	47	3.859^{ab}	111.3	161.0^a	15.42^b	11.70^b	3.72^b	1.47^a	4.91
EXP[3]	46	3.917^a	110.6	158.2^b	16.85^a	12.91^a	3.95^a	1.49^a	4.30
SEM		0.043	0.5	1.0	0.23	0.20	0.08	0.04	0.20
Age at photostimulation									
20 wk	70	3.844	110.8	158.2	15.89	12.12	3.77	1.49^a	4.76
23 wk	71	3.849	110.6	156.8	15.79	12.00	3.79	1.41^b	4.60
SEM		0.035	0.4	0.8	0.19	0.16	0.06	0.03	0.16
		Probability							
Source of variation									
Strain		0.037	0.309	0.0001	0.0001	0.0001	0.031	0.036	0.064
Age at photostimulation		0.922	0.622	0.220	0.604	0.604	0.814	0.042	0.468
Interaction		0.309	0.637	0.592	0.407	0.841	0.488	0.488	0.634

[1] Breast weight: *Pectoralis major* and *Pectoralis minor* weight.

[2] FSY: Arbor Acres Feather Sexable Yield.

[3] EXP: Arbor Acres experimental line selected for increased breast muscle yield.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

Table 3-14. Ovarian parameters measured at 53 wk of age on three strains of female broiler breeders, photostimulated at either 20 or 23 wk of age

	Reproductive parameters		
Source	Oviduct	Ovary	Stroma
	g	g	g
Strain			
Classic	71.3	58.5	9.07
FSY[1]	71.8	62.3	9.54
EXP[2]	70.8	65.9	9.60
SEM	1.5	2.3	0.31
Age at photostimulation			
20 wk	70.1	59.6^{b}	9.21
23 wk	72.5	64.9^{a}	9.60
SEM	1.2	1.9	0.25
Interaction			
Classic × 20 wk	68.8^{b}	53.7^{b}	9.01
FSY × 20 wk	68.8^{b}	65.1^{ac}	9.53
EXP × 20 wk	72.7^{ab}	60.1^{bc}	9.10
Classic × 23 wk	73.8^{ab}	63.3^{ac}	9.14
FSY × 23 wk	74.9^{a}	59.6^{bc}	9.56
EXP × 23 wk	68.9^{b}	71.7^{a}	10.10
SEM	2.1	3.3	0.44
	----------------------------------	-Probability-	----------------------------------
Source of Variation			
Strain	0.874	0.078	0.400
Age at photostimulation	0.149	0.048	0.269
Interaction	0.032	0.016	0.459

[1] FSY: Arbor Acres Feather Sexable Yield.

[2] EXP: Arbor Acres experimental line selected for increased breast muscle yield.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

Table 3-15. The number of follicles and atretic follicles measured at 53 wk of age on female broiler breeders of one of three strains photostimulated at either 20 or 23 wk of age

	Number of ovarian follicles		Number of atretic follicles	
Source	SYF[1]	LYF[2]	SYF[3]	LYF[4]
	#	#	#	#
Strain				
Classic	11.65	5.13	3.52	0.28
FSY[5]	11.07	5.28	3.62	0.39
EXP[6]	12.56	5.49	3.86	0.26
SEM	0.85	0.15	0.37	0.13
Age at photostimulation				
20 wk	11.65	5.10^{b}	3.71	0.19
23 wk	11.87	5.49^{a}	3.62	0.43
SEM	0.69	0.12	0.30	0.10
	----------Probability----------			
Source of Variation				
Strain	0.451	0.239	0.796	0.730
Age at photostimulation	0.826	0.029	0.826	0.108
Interaction	0.108	0.231	0.481	0.269

[1] SYF: Small yellow yolk-filled follicles between 5 and 10 mm in diameter.

[2] LYF: Large yellow yolk-filled follicles greater than 10 mm in diameter.

[3] Atretic SYF: atretic small yellow follicles; follicles between 5 and 10 mm in diameter, characterized by a shrunken and/or discolored appearance.

[4] Atretic LYF: atretic large yellow follicles; follicles greater than 10 mm in diameter, characterized by a shrunken and/or discolored appearance.

[5] FSY: Arbor Acres Feather Sexable Yield.

[6] EXP: Arbor Acres experimental line selected for increased breast muscle yield.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

3.4 REFERENCES

Anonymous, 1998. Arbor Acres Broiler Breeder Management Manual. Arbor Acres Farms Inc., Glastonbury, CT, USA.

Bahr, J. M., and A. L. Johnson, 1984. Regulation of the follicular hierarchy and ovulation. J. Exp. Zool. 232: 495-500.

Brody, T. B., P. B. Siegel, and J. A. Cherry, 1984. Age, body weight and body composition requirements for the onet of sexual maturity of dwarf and normal chickens. Br. Poult. Sci. 25: 245-252.

Canadian Council on Animal Care, 1984. Guide to the Care and Use of Experimental Animals.Vol. 2. Canadian Council on Animal Care, Ottawa, ON, Canada.

Eitan, Y., and M. Soller, 1996. Selection for high and low threshold body weight at first egg in broiler strain females. 6. Threshold body weight for onset of photosensitivity in females of the selection lines. Poultry Sci. 75:459-463.

Frank, F. R., M. H. Swanson, and R. E. Burger, 1964. The relationship between selected physical characteristics and the resistance to shell failure of Gallus domesticus eggs. Poultry Sci. 43:1228-1235.

Gilbert, A. B., M. M. Perry, D. Waddington, and M. A. Hardie, 1983. Role of atresia in establishing the follicular hierarchy in the ovary of the domestic hen (*Gallus domesticus*). J. Reprod. Fert. 69: 221-227.

Gilbert, A. B., and J. W. Wells, 1984. Structure and function of the ovary. Pages 15-27 *in:* Reproductive Biology of Poultry. F. J. Cunningham, P. E. Lake, and D. Hewitt, ed. British Poultry Science Ltd., Longman Group, Harlow, England.

Goonewardene, L. A. and L. Z. Florence, 1992. The need for the analysis of treatment × period interactions in animal experiments. Pages 265-279 *in*: Proc. of the Kansas State University Conf. on Applied Statistics in Agriculture. G. Milliken and J. Schwenke, ed.

Harrison, P. C., G. Schumaier, and J. McGinnis, 1969. Reproductive development and response of white leghorn pullets subjected to increasing day-lengths at different ages. Poultry Sci. 48: 1021-1026.

Hocking, P. M., 1996. Role of body weight and food intake after photostimulatin on ovarian function at first egg in broiler breeder females. Br. Poult. Sci. 37:841-851.

Jaap, R. G., and F. V. Muir, 1968. Erratic oviposition and egg defects in broiler-type pullets. Poultry Sci. 47:417-423.

Joseph, N. S., N. A. Robinson, R. A. Renema, and F. E. Robinson, 1999. Shell quality and color variation in broiler breeder eggs. J. Appl. Poultry Res. 8:70-74.

Katanbaf, M. N., E. A. Dunnington, and P. B. Siegel, 1989. Restricted feeding early and late-feathering chickens. 2. Reproductive responses. Poultry Sci. 68:352-358.

Leeson, S., R. J. Etches, and J. D. Summers, 1988. Development of Leghorn pullets subjected to early light stimulation. Can. J. Anim. Sci. 68:1267-1275.

Leeson, S., and J. D. Summers, 1983. Consequence of increased feed allowance for growing broiler breeder pullets as a means of stimulating early maturity. Poultry Sci. 62:6-11.

McDaniel, G. R., J. Brake, and M. K. Eckman, 1981. Factors affecting broiler breeder performance. 4. Interrelationship of some reproductive traits. Poultry Sci. 60:1792-1797.

Robinson, F. E., and R. J. Etches, 1986. Ovarian steroidogenesis during follicular maturation in the domestic fowl (*Gallus domesticus*). Biol. Reprod. 35:1096-1105.

Robinson, F. E., R. T. Hardin, and A. R. Robblee, 1990. Reproductive senescence in domestic fowl: effects on egg production, sequence length and inter-sequence pause length. Br. Poult. Sci. 31:871-879.

Robinson, F. E., N. A. Robinson, and T. A. Scott, 1991. Reproductive performance, growth and body composition of full-fed versus feed-restricted broiler breeder hens. Can. J. Anim. Sci. 71:549-556.

Robinson, F. E., J. L. Wilson, M. W. Yu, G. M. Fasenko, and R. T. Hardin, 1993. The relationship between body weight and reproductive efficiency in meat-type chickens. Poultry Sci. 72:912-922.

Robinson, F. E., T. A. Wautier, R. T. Hardin, N. A. Robinson, J. L. Wilson, M. Newcombe, and R. I. McKay, 1996. Effects of age at photostimulation on reproductive efficiency and carcass characteristics. 1. Broiler breeder hens. Can. J. Anim. Sci. 76:275-282.

SAS Institute Inc., 1999. The SAS System for Windows, NT Version 4.0.1381. SAS Institute Inc., Cary, NC, 27513, USA.

Siegel, P. B., and E. A. Dunnington, 1985. Reproductive complications associated with selection for broiler growth. Br. Poult. Sci. 26: 59-72.

Soller, M., T. Brody, Y. Eitan, T. Agurksy, and C. Wexler, 1984. Minimum weight for the onset of sexual maturity in female chickens: heritability and phenotypic and genetic correlations with early growth rate. Poultry Sci. 63:2103-2113.

Yuan, T., R. J. Lien, and G. R. McDaniel, 1994. Effects of increased rearing period body weights and early photostimulation on broiler breeder egg production. Poultry Sci. 73:792-800.

Zelenka, D. J., P. B. Siegel, E. A. Dunnington, and J. A. Cherry, 1986. Inheritance of traits associated with sexual maturity when populations of chickens reach 50% lay. Poultry Sci. 65:233-240.

4.0 CARCASS CHARACTERISTICS AND REPRODUCTIVE PERFORMANCE OF BROILER BREEDER FEMALES IN RESPONSE TO A MID-CYCLE INCREASE IN PHOTOPERIOD

4.1 INTRODUCTION

Chickens in temperate climates interpret a change in photoperiod as a change in the seasons that govern the reproductive cycle in that reproductive function is stimulated as day length increases from the winter solstice to the summer solstice (Farner, 1964). Chickens can be reared indoors under artificial lighting conditions so that the breeding season is not negatively affected by seasonal changes in day length. Typically, chicks are reared under a 'short day length' such as 8 h of light/d. Once the birds have reached adequate age, BW, and body composition, day length is increased to simulate the increasing day lengths of spring and summer (i.e. 14 h of light/d). This "photostimulation" cues a cascade of physiological responses, which lead to sexual maturation and reproductive competance. Simplistically, holding birds on the same 'stimulatory' day length extends the breeding season indefinitely.

The rate of egg production declines as the broiler breeder hen ages. This is caused by a decrease in the rate of follicular recruitment compared to younger hens (less than 1-yr old) resulting in fewer large yellow follicles (LYF) on the ovary (Williams and Sharp, 1978). The time needed for a follicle to reach an ovulable state is also increased as the hen ages (Bahr and Palmer, 1989). Sharp et al. (1992) suggested that the reduction in egg production that occurred as the hen aged was partially caused by the development of photorefractoriness. Photorefractoriness refers to a lack of response to the long-day photoperiod (Nicholls et al., 1988). Photorefractoriness has been associated with a decrease in hypothalamic gonadotropin-releasing hormone (GnRH) concentration in both European starlings (Dawson et al., 1985) and egg-type hens (Sharp et al., 1990).

One alternative to removing an egg-layer flock at the end of a production cycle is to induce the flock to molt. This is achieved by imposing a period of short day lengths coupled with nutrient restriction. This combination of factors serves to restore the hen's sensitivity to long day lengths. When the day length is again increased, the birds respond by laying eggs at a higher rate than before the forced molt. As yet, this is the only known way to intentionally dissipate photorefractoriness and regain ovarian function. Sharp (1993) proposed an alternative method, involving a further increase in photoperiod mid-way through the laying cycle. This alternative method was believed to increase GnRH output by stimulating the neuronal inputs that regulate GnRH synthesis in the hypothalamus. This would restimulate the anterior pituitary, increasing gonadotropin output. Therefore, the increase in circulating luteinizing hormone (LH) concentration would increase the rate of follicular recruitment into the LYF hierarchy and the interval between ovulations would decrease (Sharp, 1993).

The effect of a mid-cycle increase in day length was examined using dwarf broiler breeders (Sharp et al., 1992). At 28 wk of age, dwarf breeders received an increase in day length from 14 to 20 h of light/d. Sharp et al. (1992) found that these birds had a higher persistency of lay than hens that were held on 14 h of light/d. Similarly, when the day length was gradually increased from 14 to 23 h of light/d, beginning at 30 wk of age, egg-layers had a higher overall egg production (67.7%) than layers that were not given any additional light after photostimulation (61.7 to 64.5%) (Marr et al., 1962). Although not yet tested, this approach may slow the rate of decline in egg production in broiler breeders.

The first objective of this trial was to assess changes in carcass characteristics of female broiler breeders, in particular breast muscle weight and ovarian morphology, from time of photostimulation to 54 wk of age. The second objective was to determine if female broiler breeders would respond to a further increase in photoperiod after the initial photostimulation and if the reproductive response would differ between two strains of broiler breeders. The hypothesis was that an additional increase in photoperiod would stimulate an increase in ovulation rate and improve egg production and that the effects may differ for the two strains of birds.

4.2 MATERIALS AND METHODS

Stocks and Management

The University of Alberta's Faculty of Agriculture, Forestry and Home Economics Animal Policy and Welfare Committee approved this protocol according to the *Guide to the Care and Use of Experimental Animals* (Canadian Council on Animal Care, 1984). Eggs from two strains of commercial broiler breeders were obtained from Cobb-Vantress Inc.[1] For the purpose of maintaining anonymity, the strains were referred to as X and Y, respectively. These strains were believed to differ in sensitivity to light as field trials had indicated that Strain Y had lower egg production than Strain X. The eggs were incubated and hatched at a commercial hatchery.[2] Two hundred pullets of Strain X and 200 pullets of Strain Y were reared in floor pens in a light-tight facility from 0 to 6 wk of age. For the first 3 d post hatch, the photoperiod was 24 h of light/d. From 4 d to 22 wk of age, the photoperiod was decreased to 8 h of light/d.

From hatch to 3 wk of age, the pullets were fed a starter diet *ad libitum* (ME: 2783 kcal/kg; CP: 18.1%). At 3 wk of age, they were switched to a grower diet (ME: 2711 kcal/kg; CP: 14.6%). Feed allocation at this point followed a skip-two-day schedule; that is, feed allocation was based on a 7-d week but was administered on only 5-d per week. Allocation of feed was based on a mean weekly BW of each pen as it compared to the target BW in the Cobb 500 Breeder Management Guide (Anonymous, 1998). Therefore, both strains were fed according to the same BW curve. Each week when BW was determined, feed allocation was recalculated accordingly.

Experimental Design

The pullets were photostimulated at 22 wk of age by increasing the photoperiod from 8 h of light/d to 14 h of light/d (14L:10D). At 32 wk of age, a solid black curtain (made of two layers of polyethylene plastic) was placed down the center of the room. Light-tight ducting enabled air circulaton between the two sides of the room. This ensured that, despite the division of the room, the environment for all of the birds was very similar. Birds on one side of the room continued to receive a photoperiod of 14L:10D (control). The birds on the other side of the room were given an additional 30 min of light/d per week cumulatively, reaching 18 h of light/d (18L:6D) by 40 wk of age. The photoperiods remained unchanged until the trial was terminated at 54 wk of age.

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[1] Cobb-Vantress Inc., PO Box 1030, Siloam Springs, AR, USA, 72761-1030

[2] Lilydale Foods Co-operative Ltd., 7503-127 Avenue, Edmonton, AB, Canada, T5C 1R9

Experimental Fate. At 20 wk of age, all of the birds were individually weighed and the 128 pullets of each strain closest to the target BW of 2.16 kg were selected for the trial. Each bird was randomly assigned to one of five experimental fates (A, B, C-32, C-40, or C-54). The 16 A birds of each strain were killed by cervical dislocation at 22 wk of age, at the time of photostimulation. The 16 B birds of each strain were killed after sexual maturation, specifically, after their third oviposition. The remaining birds were further subdivided into three groups that were killed at 32, 40, or 54 wk of age (C-32, C-40, and C-54, respectively). The C-32 group consisted of 16 birds of each strain processed shortly after peak egg production but before the treatments began. The next group of 32 birds per strain was processed after the supplemental photostimulation was complete were in place at 40 wk of age (C-40). The last group of 48 birds per strain was processed at the end of the trial, at 54 wk of age (C-54). The C-54 group allowed for examination of changes in egg parameters throughout the entire laying cycle. All production parameters including fertility and hatchability were determined for C-54 birds only. At 22 wk of age, the B and all of the C birds were moved into individual laying cages. Individual BW were taken weekly. Feed was allocated daily based on the mean BW of the entire flock with feed allocation being identical for all of the birds.

Egg Weight and Production. When a bird achieved sexual maturity (first oviposition) the age, BW and egg weight were recorded. The first three eggs of the B birds were opened to determine if there were strain differences in yolk, albumen and shell weight. Eggs from the C-54 birds were collected daily, weighed and assigned an egg quality code. Eggs were categorized based on weight, shell quality, and the number of yolks in the egg. A normal egg had an intact shell and a single yolk. A settable egg was a normal egg that weighed over 52 g (minimum weight accepted by Canadian hatcheries). Eggs that were broken by the handler or pecked by the bird were also considered normal. Defective eggs included double yolked, soft shelled, or membranous. The assignment of a code allowed for calculation of total and settable egg production, and analysis of patterns of defective egg production. Differences in prime sequence length, average sequence length, number of sequences, pause length, and the number of ovulations were analyzed using the Egg Production and Sequence Analyzer.[3]

Fertility and Hatchability Analysis. Once the flock had achieved 80% egg production the hens were artificially inseminated at 7-d intervals with 50 µl of pooled rooster semen. Only hens that remained on the trial to 54 wk of age (C-54) were used to assess fertility and hatchability. Eggs were sorted into lots by strain and treatment and stored at 15 to 18 C and 80% relative humidity. Eggs collected over a 7-d period were incubated in a commercial hatchery.[4] The chicks that hatched from each lot were counted and the number of culls recorded. Eggs that did not hatch were opened to determine fertility status and stage of embryonic development, if applicable. A clear egg was assumed to be infertile. The fertility and hatchability data were divided into four time periods (28 to 32 wk of age, 33 to 40 wk of age, 41 to 44 wk of age, and 50 to 53 wk of age) and analyzed separately. The period of 45 to 49 wk of age was omitted because of missing data. Fertility was calculated within a lot as the number of fertile eggs per 100 eggs set in the incubator. Hatchability was calculated as the number of chicks hatched per 100 eggs set, and hatchability of fertile eggs was calculated as the number of chicks hatched per 100 fertile eggs set.

Plasma Estradiol-17β Determination. Blood samples were collected from the B, C-40 and C-54 groups to determine changes in plasma estradiol-17β concentration in response to both strain to photoperiod and differences between strains. A blood sample was taken from each B bird at 14:00 h on the day that the third egg was laid. Blood samples were taken from the C-40 birds beginning at 32 wk of age at 7 d intervals to 40 wk of age. Blood samples were collected from the C-54 birds beginning at 22 wk of age, corresponding to the age at which they were photostimulated and continuing at 28 d intervals to 54 wk of age. An additional sample was taken from the C-54 birds prior to processing. All sampling began at 13:00 h and was completed by 14:30 h. Blood samples were collected from the brachial vein using 10 mL EDTA-coated vacuum collection tubes. Samples were immediately placed on ice and then centrifuged at 2,000 × *g* for 20 min at 4 C. Plasma was stored at -30 C.

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[3] Version 3.00. Copyright © 1999. Alberta Agriculture, Food and Rural Development, #204, 7000-113 Street, Edmonton, AB, T6H 5T6, Canada.

[4] Lilydale Foods Co-operative Ltd., 7503-127 Avenue, Edmonton, AB, Canada, T5C 1R9

Plasma estradiol-17β concentration was determined by RIA[5] using duplicate 200 μL samples in five assays. The intra-assay and inter-assay coefficients of variation were 2.26% and 5.71%, respectively. Assay parallelism was determined by measuring estradiol-17β concentration in various plasma volumes as described by Renema et al. (1999). Assay sensitivity was 2.6 pg/ml. As stated by the manufacturer, the antiserum was highly specific to estradiol, with relatively low cross-reactivity to other naturally occurring steroids (Renema et al., 1999).

Carcass Parameters. Shank and keel lengths were measured on live birds as an assessment of frame size. Using a vernier caliper, shank length was determined by measuring the length of the tibiotarsus (from the top of the hock joint to the footpad) and keel length was determined by measuring the distance from the hypocleidum-clavical joint to the caudal end of the sternum. Birds were euthanatized by cervical dislocation and then weighed individually. The *Pectoralis major* and *Pectoralis minor*, liver, abdominal fat pad, ovary, and oviduct were removed from the carcass and individually weighed. Breast weight was calculated by taking the sum of the *Pectoralis major* and *Pectoralis minor* weights. Contents in the oviduct were removed before oviduct weight was determined. Follicles were grouped into categories depending on their size (Robinson and Etches, 1986) and counted. White follicles (WF) measured between 1 and 5 mm in diameter, small yellow follicles (SYF) were between 5 and 10 mm in diameter, and large yellow follicles (LYF) were those greater than 10 mm. Each LYF was individually weighed and the largest follicle was designated the first follicle to ovulate (F1). Any incidence of atretic WF, SYF, and LYF, characterized by a discolored and/or shrunken appearance, were also noted (Gilbert et al., 1983). A stroma weight was also determined by weighing the ovary after the LYF and atretic LYF had been removed.

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[5] Kit number TKE25, Diagnostic Products Corp., Los Angeles, CA 90045-5597.

The potential for multiple ovulations was assessed by assigning LYF weighing within 1 g of each other to a hierarchy position as reported by Renema et al. (1995). Collecting this data served as an indicator for potential problems with egg formation as hens can not process more than one normal egg per day. Follicles grouped together as such were assumed to be at the same stage of development and referred to as a 'multiple arrangement of follicles.' If a follicle did not weigh within 1 g of the other LYF it was referred to as a 'single arrangement.' The total number of follicles in multiple arrangements were expressed as a percentage of the total number of LYF on the ovary (% multiple arrangement). The number of hierarchies was determined by dividing the number of LYF into the total number of multiple and single arrangments.

Statistical Analysis

Pullets were assigned to a treatment and a cage in a completely randomized design. Egg production parameters were analyzed using only the eggs laid by C-54 hens. Data (excluding sequence analysis) were analyzed by two-way analysis of variance with strain and photoperiod as the main effects using the GLM procedure of SAS® (SAS Institute, 1999). The carcass data did not yield any significant findings for photoperiod; therefore, the data from all five groups were pooled and analyzed by two-way analysis of variance with strain and age as the main effects. Sequence length parameters were analyzed as a three-way analysis of variance also using the GLM procedure of SAS® (SAS Institute, 1999) with strain, photoperiod, and age as the main effects. The data were analyzed using repeated measures (split plot) analysis according to the procedure outlined by Goonewardene and Florence (1992). Strain, photoperiod, strain × photoperiod were tested against the experimental unit cage(strain × photoperiod). Differences between means were determined using the pdiff option of the LSMEANS statement of SAS® (SAS Institute, 1999). The error variation for strain and photoperiod was the variation between birds. Birds that did not lay an egg for five or more weeks were removed from the trial. Birds that were culled or found dead in their cage were also removed from the data set. A total of five birds were not included in the analysis for these reasons. The standard error of the mean (SEM) was determined by using the group with the least number of birds. Probability values in tables and figures were taken from the ANOVA table for each parameter.

4.3 RESULTS AND DISCUSSION

Carcass Characteristics

Photostimulation and Sexual Maturity. There were no differences in BW at 22 wk of age, which was expected as the pullets had been selected based on similar BW (data not shown). Breast weight was not different between the two strains. However, the *Pectoralis major* was 14.6 ± 0.3% of BW (mean ± SEM) for Strain X and was greater than the *Pectoralis major* for Strain Y pullets (13.6 ± 0.3%), which amounted to an absolute difference of 28.4 g. There were no strain differences in any other carcass parameter measured at photostimulation. Carcass and ovarian morphology at sexual maturity were determined by processing birds after they had laid three consecutive eggs. Among this population of birds, Strain X achieved sexual maturity before Strain Y (23.5 ± 1.5 and 28.1 ± 1.5 d post-lighting, respectively). Although there were no differences in BW at photostimulation, Strain X birds weighed less (2.800 ± 0.052 kg) than Strain Y birds (2.958 ± 0.052 kg) at sexual maturity. However, when age at sexual maturity was examined for the entire flock (i.e. across all five processing groups of broiler breeders) there were no differences between the two strains for age and BW at sexual maturity. Breast weight, which was not different at photostimulation, was heavier for Strain X hens than Strain Y hens (18.7 ± 0.3 and 17.9 ± 0.3%, respectively). Absolute breast weight was not different; therefore, the difference in relative breast weight was attributed to the differences in BW. Strain Y had a higher stroma weight (8.1 ± 0.4 g) than Strain X (6.2 ± 0.4 g). Presumably, this was because Strain Y had more SYF than Strain X (15.4 ± 1.6 and 10.2 ± 1.6 SYF, respectively). Despite this difference in small follicular number, the number of LYF was similar for both strains. This agreed with earlier observations in that the number of small follicles was not related to the number of large ovarian follicles (Hocking et al., 1989; Renema et al., 1999). Among the birds killed at sexual maturity there were no differences in any other ovarian parameter measured.

Of the first three eggs laid per hen, those with a single yolk and a hard, intact shell were opened to determine the weight of the shell, yolk, and albumen (Table 4-1). Mean egg weight was 4.5 ± 1.1 g heavier for Strain Y than Strain X. The difference in egg size was explained by a higher albumen weight in Strain Y eggs (27.80 ± 0.91 and 31.66 ± 0.91 g for Strain X and Y, respectively) as there were no differences in shell or yolk weight. In addition, Strain Y hens were heavier than Strain X hens; and BW is positively related to egg weight (McDaniel et al., 1981; Summers and Leeson, 1983; Spratt and Leeson, 1987). As a percentage of egg weight, shell weight was higher for Strain X than Strain Y (8.92 ± 0.21 and 8.02 ± 0.21%, respectively). This was related to a higher specific gravity on Strain X eggs. Frank et al. (1964) stated that specific gravity was a good measure of shell thickness and Joseph et al. (1999) noted a positive correlation between shell weight and specific gravity, suggesting than Strain X produced thicker shelled eggs than Strain Y.

32 Wk of Age. Shortly after peak egg production, hens from both strains were processed to determine differences in carcass parameters prior to the onset of increasing the photoperiod (data not shown). At this time, there were no differences in breast or *Pectoralis major* weights. There were also no differences in stroma weight or SYF number; however, Strain X had more atretic WF than Strain Y (61.4 ± 3.3 and 51.7 ± 3.3 WF, respectively). Whereas, Strain Y had significantly more LYF that were part of a multiple arrangement than Strain X, 17.9 ± 3.7 and 1.8 ± 3.7%, respectively. The percentage of LYF in a multiple arrangement serves as an indicator of potential problems with egg formation and egg laying as does the presence of more than one hierarchy on the ovary. Strain Y hens had 1.11 ± 0.02 hierarchies on their ovary as compared to Strain X hens with only 1.01 ± 0.02 hierarchies. Although there were no differences in the number of LYF, a higher percentage of multiple arrangements would indicate that the LYF are at a similar stage of growth and maturation and thus are more likely to ovulate on the same day (Hocking et al., 1987; 1989; Yu et al., 1992). Furthermore, a decrease in the rate of atresia in the small follicular pool may increase the number of follicles recruited into the LYF hierarchy. However, a pattern between the number WF and their rate of atresia was not found (Hocking et al., 1989); therefore, a relationship between the number of large follicles and the number of atretic small follicles is not readily apparent.

40 Wk of Age. After the photoperiodic treatments were imposed, minimal changes in carcass parameters in response to the additional day length were noted (data not shown). Two differences in ovarian morphology were found. Although the number of atretic WF was higher for Strain X than Y at 32 wk of age it did not differ at 40 wk of age. The hens on 18L:6D had 66.7 ± 3.8 atretic WF compared to 57.3 ± 3.8 atretic WF for the hens on 14L:10D. This may indicate that the ovaries of the 18L:6D group responded to the further increase in day length, although there were no differences in the number WF or the numbers of SYF and LYF. The constant photoperiod of 14L:10D resulted in a higher mean LYF weight (10.3 ± 0.2 g) than the increasing photoperiod of 18L:6D (9.7 ± 0.2 g). This difference in LYF weight, although significant, was not related to any further treatment differences in the number of LYF or the weight of the ovary. Strain differences at 32 wk of age in the percentage of multiple follicles did not occur at 40 wk of age (2.6 ± 1.7 and 2.4 ± 1.7 %, for Strain X and Y, respectively).

54 Wk of Age. The strain of the hen and the photoperiod treatments had no effect on BW, shank length, keel length, breast weight, and liver weight at 54 wk of age. Abdominal fat pad weight, as a percentage of BW, was higher in Strain X versus Strain Y birds (5.05 ± 0.17 and 4.35 ± 0.17%, respectively). There were also strain differences in stroma and oviduct weight, with Strain Y having a heavier stroma and oviduct (8.65 ± 0.26 g and 71.1 ± 1.8 g, respectively) than Strain X birds (7.74 ± 0.26 g and 66.0 ± 1.8 g, respectively). It is difficult to explain these differences, as there were no subsequent effects on any other ovarian parameter. At 40 wk of age, the hens on the 18L:6D treatment had more atretic WF than hens on the 14L:10D treatment, while the opposite occurred at the end of the trial. Increasing the photoperiod to 18L:6D resulted in 73.1 ± 3.7 atretic WF, significantly less than the 87.1 ± 3.7 atretic WF under the constant treatment. As there is not enough knowledge about the relationship between atretic WF and the rate of follicle selection and maturation it is difficult to draw conclusions. The response observed at 40 wk of age to the 18L:6D photoperiod was to increase the number of atretic small follicles, perhaps in response to an increase in androgen output or an increase in growth rate among these follicles. Whereas at 54 wk of age, the opposite occurrence was observed, in that it was the 14L:10D hens that had more atretic WF. Perhaps exposure to the same photoperiod (14L:10D) from photostimulation to the end of the laying cycle may have been the cause, promoting the increase in atretic WF.

Age Effects on Carcass Characteristics. As there were few significant effects of day length treatment on carcass characteristics, all five groups of birds (A, B, C-32, C-40, and C-54) were pooled together and the data were analyzed for differences among strain and age. Differences in carcass parameters are presented in Table 4-2. There were no significant strain differences in BW, shank length, keel length, breast weight, liver weight, and abdominal fat pad weight. There were, however, age differences for all of the carcass parameters measured. As expected, BW increased as the age of the hen increased. Shank length was smaller at photostimulation (104.4 ± 0.5 mm). It increased at sexual maturity (109.3 ± 0.5 mm) and did not change significantly afterwards. At photostimulation, keel length was also small (148.1 ± 1.1 mm) but unlike shank length it continued to increase throughout the laying period reaching 160.7 ± 1.1 mm at 54 wk of age. This is unlike earlier observations in which keel length did not change after sexual maturity (Robinson et al., 1996). As the hen aged, absolute breast weight increased (data not shown), however, as a percentage of BW, it became proportionately smaller.

Relative liver weight reached a maximum at 32 wk of age (2.01 ± 0.6%) decreasing at 40 and 54 wk of age (1.80 ± 0.06 and 1.46 ± 0.06%, respectively). Leveille et al. (1975) demonstrated that the liver was the major site of lipid biosynthesis, including the lipids for yolk formation. The abdominal fat pad weight increased proportionately from 22 to 54 wk of age (0.92 ± 0.16 to 4.69 ± 0.16%). Therefore, as the hen aged, nutrients were diverted away from protein deposition for muscle growth and into liver lipid and fat storage.

With all groups of birds pooled together, there were strain differences for some of the reproductive parameters measured (Table 4-3). Oviduct weight was significantly higher for Strain Y than X (54.5 ± 0.9 and 51.8 ± 0.9 g, respectively). Strain Y also had a larger stroma weight and a higher number of SYF than Strain X. Oviduct weight also increased from 22 wk of age to 32 wk of age. This was expected as BW was also increasing during this time. Oviduct weight remained unchanged from 32 to 54 wk of age, suggesting that once peak egg production was achieved the size of the oviduct did not change. As a percentage of BW, oviduct weight increased from 0.02 ± 0.05% at 22 wk of age to 2.16 ± 0.05% at sexual maturity, and then declined to 1.84 ± 0.05% by 40 wk of age. This suggests that the oviduct is a priority tissue for nutrient partitioning during sexual maturation because it reaches a mature weight before the rest of the bird stops growing. Ovary weight changed more than oviduct weight, increasing to 67.0 ± 1.9 g at sexual maturity but then decreasing to 54.7 ± 1.9 g by 54 wk of age. Mean LYF weight increased as the processing age increased reaching a maximum value at 40 wk of age (10.01 ± 0.19 g). At sexual maturity the broiler breeders in this trial had a mean of 8.78 ± 0.20 LYF on their ovary. At 32 and 40 wk of age, this number had declined to 6.16 ± 0.20 and 5.60 ± 0.20 LYF, respectively. Although mean LYF weight did not change after 40 wk of age, at 54 wk of age the number of LYF had decreased to 4.60 ± 0.20. Williams and Sharp (1978) also noted a decrease in the number of LYF in older hens. Although the number of WF and SYF did not change, the incidence of atresia among the WF and SYF increased as the hen aged. The number of atretic LYF decreased from sexual maturity to 54 wk of age.

Figure 4-1 outlines the change in *Pectoralis major* weight from photostimulation (22 wk of age) to 54 wk of age for each strain. As a percentage of BW, Strain Y pullets had a heavier *Pectoralis major* than Strain X pullets at 22 wk of age. From sexual maturity to 54 wk of age, *Pectoralis major* weight, as mentioned earlier, decreased with age but was not different among strains. At 54 wk of age, Strain X hens had a higher abdominal fat pad weight than Strain Y hens (5.04 ± 0.13 and 4.35 ± 0.13 %, respectively) (Figure 4-2). Strain Y hens had more LYF than Strain X at sexual maturity than at 32, 40, or 54 wk of age (Figure 4-3). Prior to sexual maturity, ovary weight was similar for the two strains (Figure 4-4). By sexual maturity (as with LYF number), Strain Y had a higher ovary weight (72.3 ± 4.7 g) than Strain X (61.7 ± 4.7 g). As Strain Y achieved a mature breast weight sooner than Strain X, presumably Strain Y hens were able to prepare for reproductive development and function before Strain X hens. At 32 and 40 wk of age, there were no differences in ovary weight, but at 54 wk of age the ovaries from Strain X birds weighed more than from Strain Y birds (57.0 ± 1.8 and 52.4 ± 1.8 g, respectively). This may have also been related to the higher abdominal fat pad weight in Strain X birds.

Body Weight

At 20 wk of age, all of the pullets selected for the trial were of a BW that was less than 1% under the recommended target BW for that age (1.981 kg compared to 2.000 kg, respectively) (Figure 4-5). At 22 wk, when the pullets were photostimulated, they weighed 10% less than what was recommended (2.135 kg compared to 2.360 kg, respectively). Although feed allocation was increased in order to increase the BW of the flock, the birds remained under weight for the early lay period of the trial and did not achieve the target BW until 32 wk of age.

Both strains of broiler breeders maintained a similar weekly BW throughout the trial, as feed allocation was identical for the entire flock. Likewise, there were no treatment differences in BW from 20 to 40 wk of age. However, beginning at 41 wk of age, hens on the 14L:10D treatment weighed more than the hens on the 18L:6D treatment. This trend continued to 48 wk of age, after which BW was no longer different. One explanation for this occurrence was that the birds on the longer day were active for an additional 4 h per day than the birds on the shorter day length. Increased activity would result in the utilization of energy that is reserved for maintenance requirements leading to a decrease in BW. The difference in BW from 41 to 48 wk of age did not coincide with any changes in carcass components, as BW from 49 to 54 wk of age was similar for both treatments towards the end of the trial.

Egg Weight

Changes in mean egg weight over the trial are presented in Table 4-4. The data were analyzed separately by three different periods over the laying cycle. During the early lay period of 24 to 32 wk of age, Strain Y achieved an egg size of 54.2 ± 0.5 g. This was significantly higher than the mean egg weight of Strain X hens during this period (52.4 ± 0.5 g). Differences in egg weight between the two strains carried through the mid-laying period of 33 to 40 wk of age and the late lay period of 41 to 54 wk of age. Overall, the mean egg weight for Strain X and Y hens was 59.2 ± 0.5 and 60.9 ± 0.5 g, respectively. Providing an additional 4 h of light/d after peak egg production had no effect on egg size. Likewise, there were no differences between the interaction of strain and photoperiod (data not shown).

Egg Production

Weekly hen-day egg production was examined in a similar manner as egg weight using three laying periods (Table 4-5). Despite differences in egg size between Strains X and Y, there were no strain differences in hen-day egg production (Figure 4-6). Photoperiod treatment had no effect on egg production. This is in contrast to previous studies that observed an increase in the rate of egg production in birds that experienced a mid-cycle increase in day length (Marr et al., 1962; Sharp et al., 1992). It is possible that a similar effect was not observed in this study because both strains of broiler breeders had a high rate of egg production throughout the entire trial as evidenced by a peak egg production of approximately 93.0 ± 2.3%. As such, lengthening the photoperiod at 33 wk of age was unlikely going to slow the rate of decline in egg production further. This level of egg production is uncommon for meat-type hens, and may be attributed to their low BW during the early-lay period. However, correlation analysis showed that there was no direct relationship with early BW and total egg number (r = 0.14; P = 0.1849). Also, early BW was not directly related to relative peak egg production most likely because birds of uniform BW were selected for the trial.

Laying sequence analysis did not reveal any significant findings (Table 4-6). Total egg number (normal and defective) and normal egg number were not influenced by the strain of the hen or the photoperiod treatment (Table 4-7). The number of settable eggs (normal eggs weighing over 52 g) was different with Strain Y producing seven more eggs per hen than Strain X. This can be explained in part by the early differences in egg weight from 24 to 32 wk of age. During this time, Strain Y produced five more settable eggs per hen than Strain X (28.9 ± 1.5 and 24.0 ± 1.5 eggs, respectively). Photoperiod or the interaction of strain and photoperiod did not affect the number of ovulations per hen. This was supported by a lack of photoperiodic effect on hen-day egg production and egg numbers.

Fertility and Hatchability

Fertility and hatchability data from 28 to 53 wk of age are presented in Table 4-8. The percentage of fertile eggs was high for both strain and treatment. There were no strain or treatment effects on hatchability of fertile eggs and hatchability of all eggs set in the incubator. For the first three time periods (28 to 44 wk of age, inclusive), there were no differences in any of the fertility and hatchability parameters. However, the last 4 weeks of data revealed significant treatment effects (Table 4-8). From 50 to 53 wk of age, Strain X birds had a higher percentage of fertile eggs than Strain Y (93.1 ± 0.8 and 87.8 ± 0.8 %, respectively). Strain X also had a higher hatchability of eggs set than Strain Y. Strain Y hens on the 18L:6D photoperiod had lower fertility than the other combinations of strain and photoperiod. The hatchability of eggs set was approximately 10% lower for Strain Y hens on the 18L:6D photoperiod than for any other strain by photoperiod interaction. All of the hens were inseminated at the same time using pooled rooster semen and as there were no interaction differences in any other egg production parameter, it is difficult to explain the differences observed in hatchability of egg set.

Plasma Estradiol-17β Concentration

At sexual maturity, the Strain X birds had 74.2 ± 6.8 pg of estrogen/ml plasma and Strain Y birds had 92.4 ± 6.8 pg of estrogen/ml plasma, which was not different. Blood samples taken at 28-d intervals from photostimulation to the end of the trial (C-54 birds) did not reveal any significant effects of treatment (data not shown). Blood samples taken at 7-d intervals from 33 to 40 wk of age revealed some differences (C-40 birds). At 38 wk of age, hens receiving an increase in photoperiod had a mean plasma estradiol-17β concentration of 121.5 ± 5.6 pg/ml compared to 105.9 ± 5.6 pg/ml for hens that remained on the control photoperiod (Figure 4-7). At this age, the photoperiod for this treatment was 17L:7D. After this, there were no differences in plasma estradiol-17β level between the two treatments.

At 36 and 40 wk of age, during the time that the photoperiod was increasing, estradiol-17β concentrations were higher for Strain X than for Strain Y (Figure 4-8). Over the entire 33 to 40 wk of age period when the photoperiod was being increased by 4 h in 30-min weekly increments, Strain X had a significantly higher plasma estradiol-17β concentration than Strain Y (118.4 and 108.1 ± 3.7 pg/ml, respectively). It is difficult to explain this strain difference as Strain X hens did not have a higher rate of egg production than Strain Y hens.

The hypotheses that broiler breeder females would respond to a mid-cycle incease in photoperiod and that the response would differ for the two strains were rejected. The differences in atretic WF number at 40 and 54 wk of age and the higher level of plasma estradiol-17β at 38 wk of age suggests that there may have been some physiological responses to the increase in photoperiod. However because the hens used in this trial performed better than expected (93.0% peak egg production), any further increase in photoperiod was unlikely going to improve this production rate. This high level of egg production can not be explained. The decrease in BW below the recommended target early in lay did not adversely affect egg production. Future considerations may include providing the mid-cycle increase at the time of peak egg production (29 to 30 wk of age) or waiting until 40 wk of age, when LYF numbers and the rate of egg production begins to decline. Despite no significant effects of photoperiod on carcass or egg parameters, there were some interesting patterns connected with age and strain. The results from this study would suggest that frame size and breast muscle fleshing is established by sexual maturity yet organ and tissue weights are constantly changing in response to the reproductive state of the bird. Body weight increased throughout lay; however breast muscle weight, as a proportion of BW, decreased. Zelenka et al. (1986) noted that a minimum percentage of breast muscle was necessary prior to the onset of lay as an energy reserve for egg production. In the present study, once the birds commenced lay breast muscle deposition and skeletal growth (as assessed by shank and keel lengths) became secondary in priority as nutrients were partitioned into oviduct, liver, abdominal fat pad, and LYF weight.

Table 4-1. **Specific gravity, shell weight, yolk weight, albumen weight, and haugh unit measurements taken from the first three eggs[1] laid by two strains of broiler breeders processed at sexual maturity (B birds[2])**

Source	Egg weight	Specific gravity	Shell weight	Shell percentage	Yolk weight	Yolk percentage	Albumen weight	Albumen percentage	Haugh unit
	g		g	%	g	%	g	%	mm
Strain									
X	42.5^{b}	1.0826^{a}	3.77	8.92^{a}	10.95	25.84	27.80^{b}	65.22^{b}	9.83
Y	47.0^{a}	1.0768^{b}	3.76	8.02^{b}	11.57	24.75	31.66^{a}	67.19^{a}	9.58
SEM	1.1	0.0016	0.10	0.21	0.27	0.55	0.91	0.64	0.34
	----------	----------	----------	----------	-Probability-	----------	----------	----------	----------
Source of variation									
Strain	0.004	0.012	0.920	0.004	0.099	0.148	0.003	0.027	0.602

[1] First three eggs: only those with a single yolk and a hard, intact shell were used to determine egg characteristics.

[2] 'B birds': birds were killed after laying the first three eggs.

[a,b] Means within a column with no common superscript differ significantly ($P \leq 0.05$).

Table 4-2. BW and carcass characteristics of two strains of broiler breeders at five different ages throughout lay

	Carcass parameters							
Source	BW at processin	Shank length	Keel length	Breast weight[1]	*Pectoralis major* weight	*Pectoralis minor* weight	Liver weight	Abdominal fat pad weight
	kg	mm	mm	%	%	%	%	%
Strain								
X	3.181	108.9	156.0	17.6	13.3	4.32	1.74	2.91
Y	3.234	108.5	156.1	17.7	13.4	4.28	1.81	2.80
SEM	0.022	0.3	0.6	0.1	0.1	0.05	0.03	0.09
Age								
22 wk	2.207^{e}	104.4^{b}	148.1^{d}	18.5^{a}	14.1^{a}	4.43^{ab}	1.74^{b}	0.92^{e}
Sexual maturity[2]	2.879^{d}	109.3^{a}	154.4^{c}	18.3^{ab}	14.0^{a}	4.34^{ab}	1.87^{ab}	1.84^{d}
32 wk	3.369^{c}	109.5^{a}	158.3^{ab}	17.8^{b}	13.3^{b}	4.53^{a}	2.01^{a}	2.99^{c}
40 wk	3.689^{b}	110.0^{a}	158.7^{b}	16.9^{c}	12.6^{c}	4.24^{b}	1.80^{b}	3.83^{b}
54 wk	3.893^{a}	110.5^{a}	160.7^{a}	16.7^{c}	12.8^{c}	3.95^{c}	1.46^{c}	4.69^{a}
SEM	0.040	0.5	1.1	0.3	0.2	0.09	0.06	0.16
					Probability			
Source of variation								
Strain	0.090	0.364	0.885	0.712	0.485	0.597	0.106	0.387
Age	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Strain × age	0.621	0.418	0.556	0.150	0.028	0.515	0.526	0.036

[1] Breast weight: sum of the *Pectoralis major* and *Pectoralis minor* weights.

[2] Sexual maturity: hens were processed after their third oviposition.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

Table 4-3. Reproductive characteristics of two strains of female broiler breeders at five different ages throughout lay

				Number of			Number of atretic		
Source	Oviduct weight	Ovary weight	Stroma weight	WF[1]	SYF[2]	LYF[3]	WF[1]	SYF[2]	LYF[3]
	g	g	g						
Strain									
X	51.8^{b}	49.1	7.95^{b}	13.19	10.55^{b}	6.13	68.18	1.94	0.11
Y	54.5^{a}	50.3	8.75^{a}	14.27	12.48^{a}	6.44	64.20	2.35	0.21
SEM	0.9	1.1	0.19	0.64	0.52	0.12	2.60	0.36	0.04
Age									
22 wk	0.6^{c}	0.7^{d}	—	—	—	—	—	—	—
Sexual maturity[4]	62.2^{b}	67.0^{a}	7.16^{c}	—	12.79^{a}	8.78^{a}	—	0.56^{b}	0.41^{a}
32 wk	66.8^{a}	61.3^{b}	8.50^{b}	14.09	9.78^{b}	6.16^{b}	56.53^{b}	0.50^{b}	0.09^{b}
40 wk	67.8^{a}	64.8^{ab}	9.55^{a}	13.32	13.96^{a}	5.60^{c}	62.09^{ab}	4.09^{a}	0.06^{b}
54 wk	68.5^{a}	54.7^{c}	8.19^{b}	13.78	9.52^{b}	4.60^{d}	79.96^{a}	3.41^{a}	0.10^{b}
SEM	1.6	1.9	0.32	1.00	0.88	0.20	4.03	0.60	0.07
	----------Probability----------								
Source of variation									
Strain	0.044	0.466	0.010	0.239	0.009	0.073	0.278	0.416	0.083
Age	0.0001	0.0001	0.0001	0.800	0.0001	0.0001	0.0001	0.0001	0.001
Strain × age	0.019	0.356	0.155	0.897	0.139	0.012	0.371	0.598	0.316

[1] WF: white follicles (2 to 5 mm in diameter).

[2] SYF: small yellow follicles (5 to 10 mm in diameter).

[3] LYF: large yellow follicles (greater than 10 mm in diameter).

[4] Sexual maturity: hens were processed after their third oviposition.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

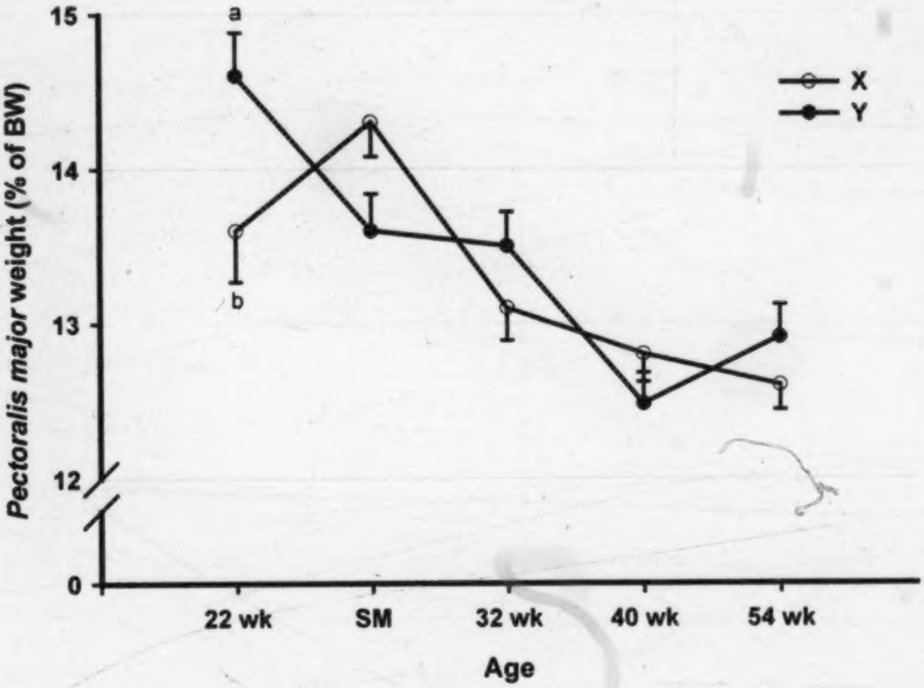

Figure 4-1. *Pectoralis major* weight (mean ± SEM), as a percentage of BW, of two strains of broiler breeders (X and Y) throughout the laying cycle; SM: sexual maturity (P=0.028). [a,b] Means within an age with no common superscript differ significantly ($P \leq 0.05$).

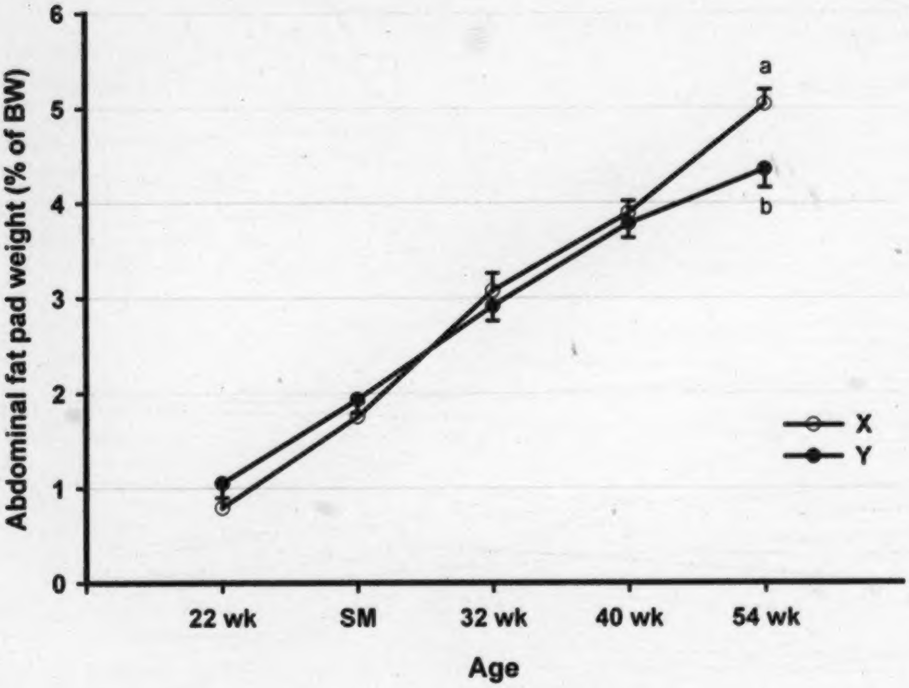

Figure 4-2. Abdominal fat pad weight (mean ± SEM), as a percentage of BW, of two strains of broiler breeders (X and Y) measured throughout the laying cycle; SM: sexual maturity (P=0.036). ^{a,b} Means within an age with no common superscript differ significantly ($P \leq 0.05$).

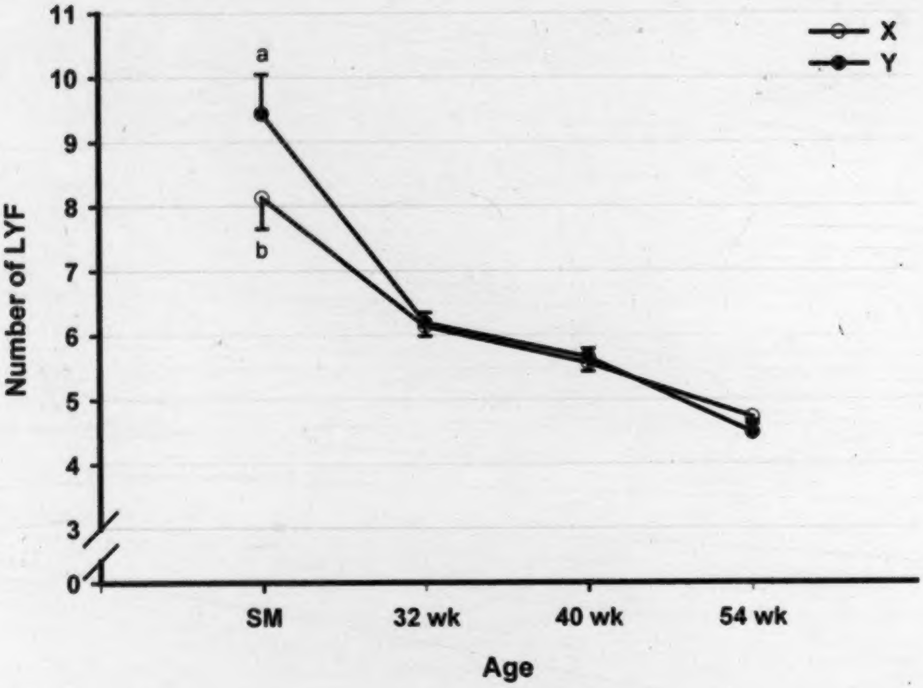

Figure 4-3. The mean number (± SEM) of large yellow follicles (LYF) of two strains of broiler breeders (X and Y) throughout lay; SM: sexual maturity (P=0.012). ^{a,b} Means within an age with no common superscript differ significantly ($P \leq 0.05$).

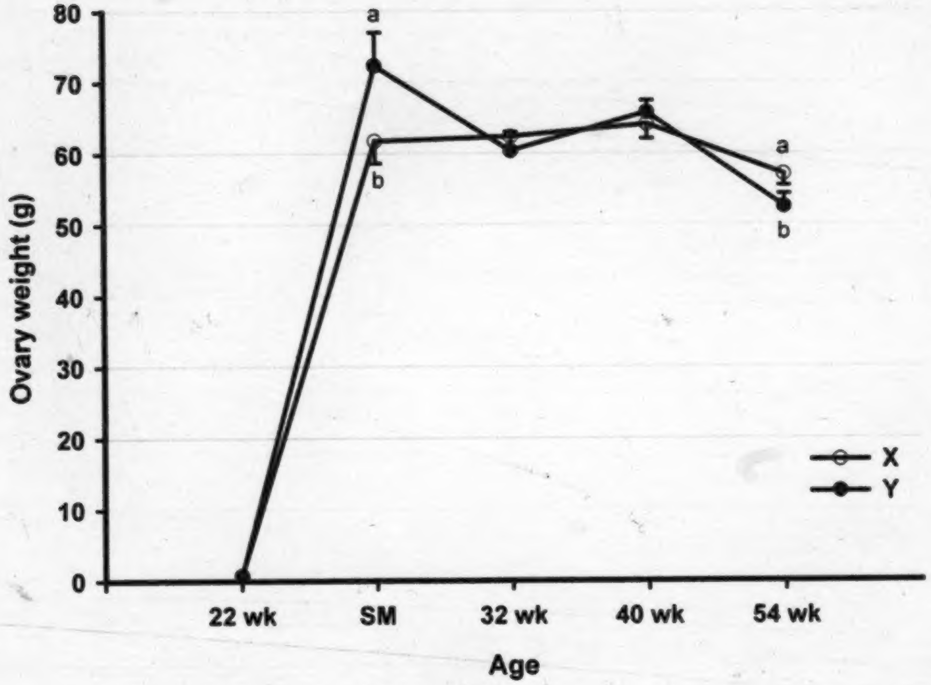

Figure 4-4. Ovary weight (mean ± SEM) at 22 wk of age, sexual maturity (defined as third oviposition), 32, 40, and 54 wk of age of two strains of broiler breeders (X and Y) (P=0.019). ^{a,b} Means within an age with no common superscript differ significantly ($P \leq 0.05$).

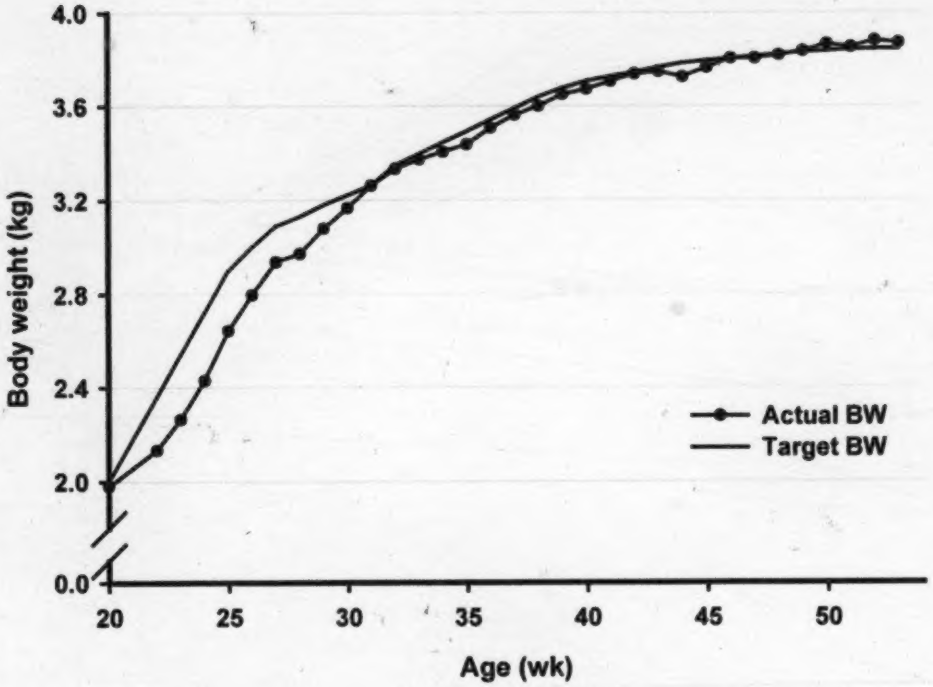

Figure 4-5. Mean weekly BW of female broiler breeders (solid line, closed circle) from 20 to 54 wk of age as compared to the target BW (solid line) as recommended by the Cobb 500 Breeder Management Guide (Anonymous, 1998).

Table 4-4. Mean weight of eggs during the early, mid, and late laying periods from two strains of broiler breeders on two photoperiods

	Egg weight[1]		
Source	Early lay period[2] (24 to 32 wk of age)	Mid lay period (33 to 40 wk of age)	Late lay period (41 to 54 wk of age)
	g	g	g
Strain			
X	52.4^b	59.5^b	63.7^b
Y	54.2^a	61.2^a	65.1^a
SEM	0.5	0.5	0.5
Photoperiod			
14L:10D	---	60.4	64.4
18L:6D	---	60.3	64.4
SEM	---	0.5	0.5
	---------- Probability ----------		
Source of variation			
Strain	0.008	0.012	0.041
Photoperiod	---	0.947	0.948
Interaction	---	0.841	0.687

[1] Egg weight: only eggs with a single yolk and a hard, intact shell were used to determine mean egg weight.

[2] Early lay period: only data for strain effects were analyzed as the photoperiodic treatments were not in place at this time.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

Table 4-5. Weekly hen-day egg production during the early, mid, and late laying periods of two strains of broiler breeders on two photoperiods

	Egg production[1]		
Source	Early lay period[2] (24 to 32 wk of age)	Mid lay period (33 to 40 wk of age)	Late lay period (41 to 54 wk of age)
	%	%	%
Strain			
X	75.0	81.5	68.9
Y	72.9	80.2	68.8
SEM	1.5	1.1	1.3
Photoperiod			
14L:10D	---	80.2	67.9
18L:6D	---	81.6	69.8
SEM	---	1.1	1.2
	Probability		
Source of variation			
Strain	0.300	0.410	0.969
Photoperiod	---	0.367	0.253
Interaction	---	0.421	0.240

[1] Egg production: all eggs, including defective eggs, were used in the calculation of hen day egg production.

[2] Early lay period: only data for strain effects were analyzed as the photoperiodic treatments were not in place at this time.

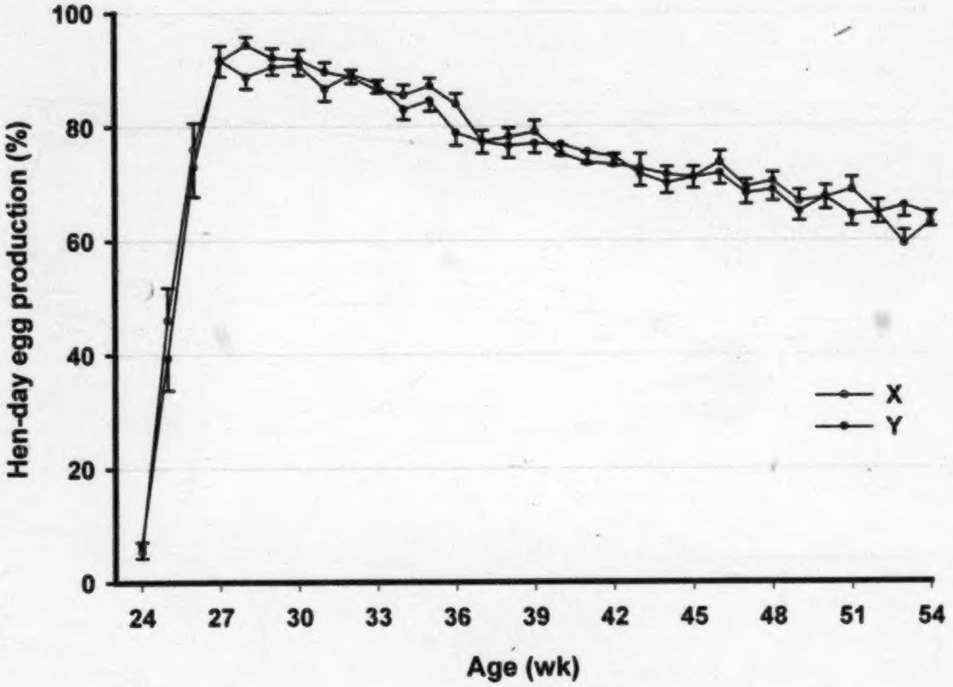

Figure 4-6. Mean (± SEM) weekly hen-day egg production for two strains (X and Y) of commercial broiler breeders from 24 to 54 wk of age. Both strains achieved a peak egg production of approximately 93.0 ± 2.3%. Strain X maintained over 80% egg production for 10 wks and Strain Y for 9 wk. [a,b] Means within an age with no common superscript differ significantly (*P*≤0.05).

Table 4-6. Laying sequence parameters measured from 24 to 54 wk of age on two strains of broiler breeders on two photoperiod treatments

	Sequence parameters measured			
Source	Prime sequence length[1]	Average sequence length	Number of sequences	Average pause length
	d	d	#	d
Strain				
X	23.9	4.03	41.6	1.14
Y	21.0	3.90	43.0	1.14
SEM	2.0	0.17	1.4	0.02
Photoperiod				
14L:10D	---	3.81	44.0	1.13
18L:6D	---	4.12	40.6	1.15
SEM	---	0.17	1.4	0.02
Interaction				
X × 14L:10D	---	3.73	44.3	1.15
X × 18L:6D	---	4.33	38.9	1.13
Y × 14L:10D	---	3.88	43.7	1.12
Y × 18L:6D	---	3.92	42.4	1.16
SEM	---	0.25	1.9	0.03
	-------------------Probability-------------------			
Source of variation				
Strain	0.292	0.583	0.450	0.859
Photoperiod	---	0.195	0.078	0.593
Interaction	---	0.248	0.284	0.274

[1] Prime sequence length: longest sequence of eggs laid; typically laid early in lay, therefore only strain data are presented.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

Table 4-7. Cumulative total egg number, normal egg number, settable egg number, and number of ovulations per hen, from 24 to 54 wk of age

	Egg parameters			
Source	Total egg number[1]	Normal egg number[2]	Settable egg number[3]	Number of ovulations[4]
Strain				
X	160.5	154.0	131.7^{b}	161.2
Y	158.4	152.7	138.7^{a}	159.4
SEM	2.1	2.1	2.5	2.1
Photoperiod				
14L:10D	158.4	152.4	132.7	159.0
18L:6D	160.6	154.3	137.7	161.6
SEM	2.1	2.1	2.5	2.1
Interaction				
X × 14L:10D	157.4	151.2	127.0	157.5
X × 18L:6D	163.7	156.9	136.3	164.8
Y × 14L:10D	159.4	153.5	138.3	160.4
Y × 18L:6D	157.4	151.8	139.1	158.3
SEM	3.0	3.0	3.5	3.0
	------------Probability------------			
Source of variation				
Strain	0.474	0.643	0.050	0.544
Photoperiod	0.464	0.510	0.231	0.388
Interaction	0.160	0.224	0.281	0.120

[1] Total egg number: calculated by counting the number of eggs laid per hen (included both defective and normal eggs).

[2] Normal egg number: calculated by counting the number of eggs with a single yolk and hard, intact shell.

[3] Settable egg number: calculated by counting the number of eggs with a single yolk and a hard intact shell, weighing over 52.0 g. Eggs with a hard shell but broken were not included in the analysis.

[4] Number of ovulations: calculated by counting the number of yolks in both defective and normal eggs laid (i.e. a double yolk egg counted as one defective egg but two ovulations).

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

Table 4-8. Fertility, hatchability of fertile eggs, and hatchability of settable eggs of two strains of broiler breeders held on 14L:10D throughout lay or given an increase in photoperiod (18L:6D) at 33 wk of age

	Hatchability parameters[1]					
	Entire laying cycle (28 to 53 wk of age)			Late-lay period (50 to 53 wk of age)		
Source	Fertility	Hatchability of fertile	Hatchability of eggs set	Fertility	Hatchability of fertile	Hatchability of eggs set
	%	%	%	%	%	%
Strain						
X	92.7	89.2	83.1	93.1^{a}	87.7	81.8^{a}
Y	90.6	88.0	80.2	87.9^{b}	86.0	76.3^{b}
SEM	0.9	1.2	1.0	0.8	1.9	1.1
Photoperiod						
14L:10D	92.5	89.1	82.9	91.4	88.1	80.9
18L:6D	90.8	88.1	80.4	89.5	85.7	77.2
SEM	0.9	1.2	1.0	0.8	1.9	1.1
Interaction						
X × 14L:10D	92.2	88.7	82.7	91.8^{a}	87.4	80.6^{a}
X × 18L:6D	92.7	89.5	83.1	91.0^{a}	86.7	83.0^{a}
Y × 14L:10D	93.1	89.7	83.5	94.4^{a}	88.0	81.1^{a}
Y × 18L:6D	88.5	86.4	77.2	84.7^{b}	83.3	71.4^{b}
SEM	1.3	1.7	1.4	1.1	2.7	1.5
	Probability					
Source of variation						
Strain	0.188	0.506	0.109	0.009	0.551	0.021
Photoperiod	0.276	0.570	0.147	0.155	0.425	0.074
Interaction	0.126	0.306	0.075	0.014	0.329	0.016

[1] Hatchability parameters: assessed by counting the number of live chicks hatched and by breaking open the hatch residue.

[a,b] Means within a column and within a source with no common superscript differ significantly ($P \leq 0.05$).

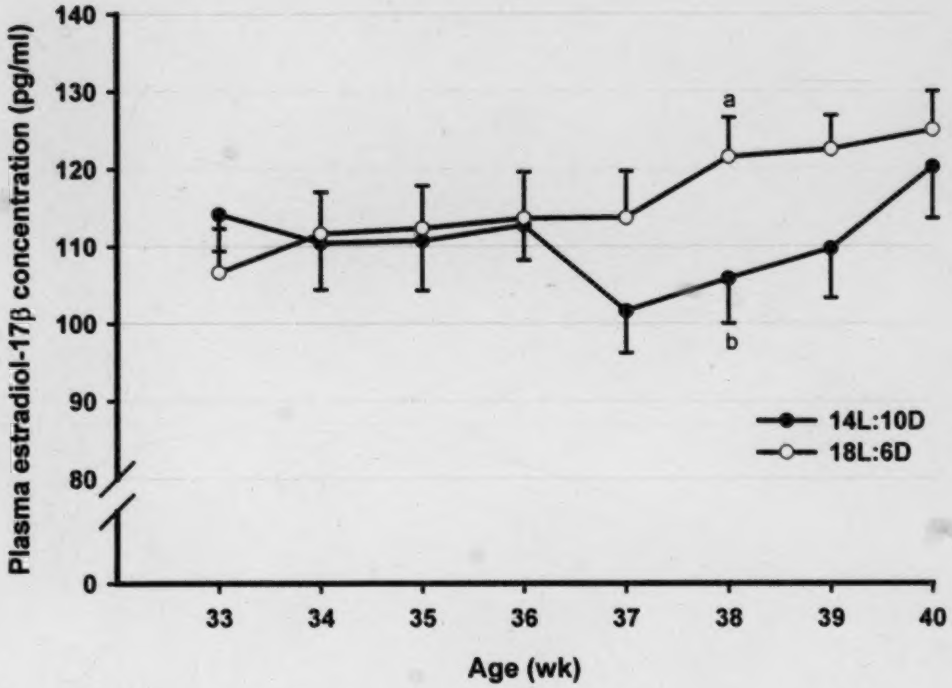

Figure 4-7. Mean (± SEM) weekly plasma estradiol-17β concentration taken from broiler breeders of one of two strains held on 14L:10D throughout lay or given an increase in photoperiod from 14L:10D to 18L:6D (in 30 minute increments per week) beginning at 33 wk of age. Overall, plasma estradiol-17β concentrations for photoperiods 14L:10D and 18L:6D were 110.6 and 116.0 pg/ml, respectively and were not significantly different (*P*=0.298). ^{a,b} Means within an age with no common superscript differ significantly ($P \leq 0.05$).

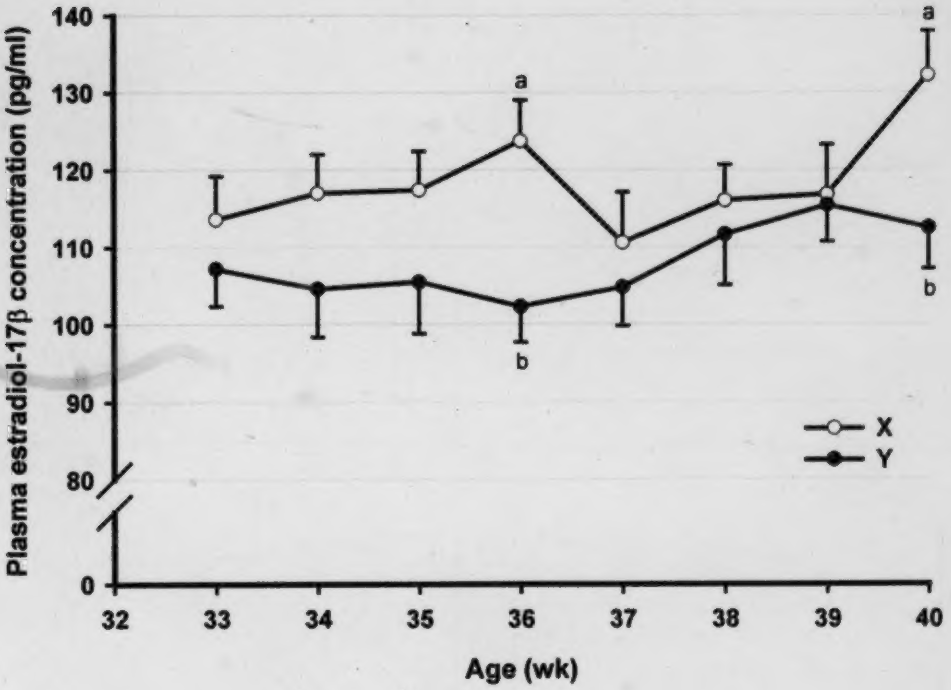

Figure 4-8. Mean (± SEM) weekly plasma estradiol-17β concentration of two strains of broiler breeders held on 14L:10D throughout lay or given an increase in photoperiod from 14L:10D to 18L:6D (in 30 minute increments per week) beginning at 33 wk of age. Overall, plasma estradiol-17β concentrations were significantly higher for Strain X (118.4 pg/ml) than for Strain Y (108.1 pg/ml; P=0.049). ^{a,b} Means within an age with no common superscript differ significantly ($P \leq 0.05$).

4.4 REFERENCES

Anonymous, 1998. The Cobb 500 Breeder Management Guide. Cobb-Vantress Inc., Siloam Springs, AR.

Bahr, J. M., and S. S. Palmer, 1989. The influence of aging on ovarian function. Critical Reviews in Poultry Biology 2:103-110.

Canadian Council on Animal Care, 1984. Guide to the Care and Use of Experimental Animals.Vol. 2. Canadian Council on Animal Care, Ottawa, ON, Canada.

Dawson, A., B. K. Follett, A. R. Goldsmith, and T. J. Nicholls, 1985. Hypothalamic gonadotropin-releasing hormone and pituitary and plasma FSH and prolactin during photostimulation and photorefractoriness in intact and thyroidectomized starlings (Sturnus vulgaris). J. Endocrinol. 105:71-77.

Farner, D., 1964. The photoperiodic control of reproductive cycles in birds. Am. Sci. 52:137-156.

Frank, F. R., M. H. Swanson, R. E. Burger, 1964. The relationship between selected physical characteristics and the resistance to shell failure of Gallus domesticus eggs. Poultry Sci. 43:1228-1235.

Gilbert, A. B., M. M. Perry, D. Waddington, and M. A. Hardie, 1983. Role of atresia in establishing the follicular hierarchy in the ovary of the domestic hen (*Gallus domesticus*). J. Reprod. Fert. 69: 221-227.

Goonewardene, L. A. and L. Z. Florence, 1992. The need for the analysis of treatment × period interactions in animal experiments. Pages 265-279 *in*: Proc. of the Kansas State University Conf. on Applied Statistics in Agriculture. G. Milliken and J. Schwenke, ed.

Hocking, P. M., A. B. Gilbert, M. Walker, and D. Waddington, 1987. Ovarian follicular structure of White Leghorns fed ad libitum and dwarf and normal broiler breeder pullets fed ad libitum or restricted until point of lay. Br. Poult. Sci. 28:495-506.

Hocking, P. M., D. Waddington, M. A. Walker, and A. B. Gilbert, 1989. Control of the development of the ovarian follicular hierarchy in broiler breeder pullets by food restriction during rearing. Br. Poult. Sci. 30:167-174.

Joseph, N. S., N. A. Robinson, R. A. Renema, and F. E. Robinson, 1999. Shell quality and color variation in broiler breeder eggs. J. Appl. Poultry Res. 8:70-74.

Leveille, G. A., D. R. Romsos, Y. Y. Yeh, and E. K. O'Hea, 1975. Lipid biosynthesis in the chick. A consideration of site of synthesis, influence of diet and possible regulatory mechanisms. Poultry Sci. 54:1075-1093.

Marr, J. E., and F. W. Garland, Jr., R. C. Eaton, and H. L. Wilcke, 1962. Effect of controlled day length during the growing and laying periods on egg production. Poultry Sci. 41:1663 (Abstract).

McDaniel, G. R., J. Brake, and M. K. Eckman, 1981. Factors affecting broiler breeder performance. 4. Interrelationship of some reproductive traits. Poultry Sci. 60:1792-1797.

Nicholls, T. J., A. R. Goldsmith, and A. Dawson, 1988. Photorefractoriness in birds and comparison with mammals. Phys. Reviews 68:133-176.

Renema, R. A., F. E. Robinson, V. L. Melnychuk, L. G. Bagley, D. A. Emmerson, and J. R. Blackman, 1995. The use of feed restriction for improving reproductive traits in male-line large white turkey hens. 2. Ovary morphology and laying traits. Poultry Sci. 74:102-120.

Renema, R. A., F. E. Robinson, J. A. Proudman, M. Newcombe, and R. I. McKay, 1999. Effects of body weight and feed allocation during sexual maturation in broiler breeder hens. 2. Ovarian morphology and plasma hormone profiles. Poultry Sci. 78:629-639.

Robinson, F. E., and R. J. Etches, 1986. Ovarian steroidogenesis during follicular maturation in the domestic fowl (*Gallus domesticus*). Biol. Reprod. 35: 1096-1105.

Robinson , F. E., T. A. Wautier, R. T. Hardin, N. A. Robinson, J. L. Wilson, M. Newcombe, and R. I. McKay, 1996. Effects of age at photostimulation on reproductive efficiency and carcass characteristics. 1. Broiler breeder hens. Can. J. Anim. Sci. 76:275-282.

SAS Institute Inc., 1999. The SAS System for Windows, NT Version 4.0.1381. SAS Institute Inc., Cary, NC, 27513, USA.

Sharp, P. J., 1993. Photoperiodic control of reproduction in the domestic hen. Poultry Sci. 72:897-905.

Sharp, P. J., I. C. Dunn, and S. Cerolini, 1992. Neuroendocrine control of reduced persistence of egg-laying in domestic hens: evidence for the development of photorefractoriness. J. Reprod. Fertil. 94:221-235.

Sharp, P. J., R. T. Talbot, G. M. Main, I. C. Dunn, H. M. Fraser, and N. S. Huskisson, 1990. Physiological roles of chicken LHRH-I and –II in the control of gonadotropin release in the domestic chicken. J. Endocrinol. 124:291-299.

Spratt, R. S., and S. Leeson, 1987. Broiler breeder performance in response to diet protein and energy. Poultry Sci. 66:683-693.

Summers, J. D., and S. Leeson, 1983. Factors influencing early egg size. Poultry Sci. 62:1155-1159.

Williams, J. B., and P. J. Sharp, 1978. Age-dependent change in the hypothalamo-pituitary-ovarian axis of the laying hen. J. Reprod. Fertil. 53:141-146.

Yu, M. W., F. E. Robinson, R. G. Charles, and R. Weingardt, 1992. Effect of feed allowance during rearing and breeding on female broiler breeders. 2. Ovarian morphology and production. Poultry Sci. 71:1750-1761.

Zelenka, D. J., P. B. Siegel, E. A. Dunnington, and J. A. Cherry, 1986. Inheritance of traits associated with sexual maturity when populations of chickens reach 50% lay. Poultry Sci. 65:233-240.

5.0 GENERAL DISCUSSION

As selection for breast muscle yield continues, hatching egg producers are faced with the challenge of ensuring adequate levels of egg production to meet the demand for broiler chickens. Therefore, proper management of the breeder flock is becoming increasingly important. The effects of different management techniques on female broiler breeders were evaluated in an attempt to address some of issues facing hatching egg producers.

1. **Strain Differences in Breeders** Determining differences between three genotypes produced by the same breeder company demonstrated how different selection pressures have changed the breeder (Joseph, Thesis: Chapter 3). The movement towards further processing has led to the creation of lines with more breast muscle than ever before. Even at similar BW, the genotype differences in *Pectoralis major* weight were evident before the trial began and continued to be different at the end of the trial. Image analysis of the *Pectoralis major* showed that the uniformity of muscle thickness has improved in the EXP line as compared to the Classic strain. This is especially important to the food industry that demands that the breast meat should be uniform to reduce variability in food preparation and provide a consistent product to the consumer. Although the EXP hens had a larger breast muscle and BW at the end of lay, reproductive performance was not greatly affected. Settable and defective egg numbers were not influenced by the strain of the bird. At 53 wk of age, the EXP hens had a similar number of LYF as the Classic or FSY hens.

There were two important strain effects on reproductive parameters. The first was that EXP hens had a shorter prime sequence length and longer pauses between sequences than Classic hens. The occurrence of arrhythmic sequences is more pronounced in selected versus unselected lines of meat-type hens (Jaap and Muir, 1968). Also, from 35 to 44 wk of age, EXP hens had a lower rate of egg production (75.7%) compared to the Classic and FSY hens (80.3 and 80.3%, respectively). One possible explanation is that the EXP birds were underweight during rearing as they were reared according FSY BW curve. Since this line has been selected for more breast muscle yield than the FSY, they may have had to be reared at a heavier BW. Consequently, the EXP hens may not have been adequately 'fleshed' to sustain a high rate of egg production. Photostimulating at 23 wk of age did not have any significant effects on the EXP hens, however, it did increase ovary weight at 53 wk of age. This suggests that delaying photostimulation gave EXP hens more time to achieve a mature BW so that once photostimulated, nutrients could be partitioned into egg output without adversely affecting growth.

2. **Increasing Early Egg Size** Egg size is particularly important to Canadian producers as eggs that are less than the 52 g threshold are considered unsettable. Generally, the first 4 to 8 eggs laid by a hen do not meet this standard set by Canadian hatcheries (F. E. Robinson, personal communication). The estimated loss in potential revenue is $1.44 to $2.95 per hen (at $0.36 per egg). Egg size is associated with BW, therefore bigger hens tend to lay larger eggs (McDaniel et al., 1981). However for broiler breeders, increased BW is usually associated with complications in egg formation caused by excess ovarian follicles (Hocking et al., 1989; Yu et al., 1992). Therefore, any method to increase egg size should also focus on maintaining appropriate BW. The NRC (1994) does not specifiy a requirement for crude protein. The Cobb 500 Breeder Management Guide recommends 15 to 16% CP in the diet (Anonymous, 1998). The effects of feeding 14, 16, and 18% dietary CP were determined (Joseph, Thesis: Chapter 2). Egg weight was increased in response to feeding 16 and 18% CP as compared to 14% CP. At 29 wk of age coincident with the time of peak egg production, the 14% CP had the lowest hen-day egg production (74.2%) compared to 89.6 and 86.5% egg production for 16 and 18% CP, respectively. Taken together, the increases in egg weight and egg production resulted in the production of four more settable eggs per hen fed the 16 or 18% CP diet. There were no differences in feeding 16% CP versus 18% CP diets. This agrees with earlier observations that egg weight and the rate of egg production can be increased when increasing levels of dietary protein are fed. However, there is an upper limit beyond which additional protein has no effect. Waldroup et al. (1976) found that there was no difference in egg production when 24 versus 22 g of protein were fed per day. Pearson and Herron (1981) also found that diets containing more

than 63 g of protein per Mcal of AME actually reduced egg production. Results from this study would indicate that increasing the dietary level of CP during the pullet-to-breeder transition period can increase early egg size. Four additional eggs per hen would equal approximately $1440 in increased revenue per 1000 hens. Further research in this area would include examining the effects of feeding 14, 16, and 18% CP throughout the entire laying cycle.

Delaying age at photostimulation increased early egg size, a by-product of increasing BW (Joseph, Thesis: Chapter 3). The hens photostimulated at 23 wk of age had a higher egg weight throughout the trial; however they produced the same number of settable eggs as those photostimulated at 20 wk of age. This result is still positive because, although delaying photostimulation by 3-wk delayed sexual maturity, it did not decrease the number of eggs produced per hen.

3. **Slowing the Rate of Decline in Egg Production as the Hen Ages** The decrease in the rate of follicular recruitment as the hen ages results in a smaller number of LYF and decreased egg production (Williams and Sharp, 1978). This decline has been attributed to the development of 'partial photorefractoriness' whereby after a period of time the hen does not respond to the stimulatory photoperiod as she did at the onset of lay (Sharp et al., 1992). An attempt was made to increase the rate of egg production by providing an increase in day length shortly after peak production (Joseph, Thesis: Chapter 4). The birds in this study laid eggs at an unusually high rate; the decline in egg production as the hen aged was slow as evidenced by a 68 to 70% weekly hen-day egg production during the late laying period. As a result, there was no effect of increased photoperiod on egg production. However, this experiment clearly demonstrated that the decrease in egg production was also a function of age itself (Joseph, Thesis: Chapter 4). The number of LYF decreased from 8.78 at sexual maturity to 4.60 at the end of the laying cycle. This too may have confounded the effects of the treatment. The plasma estradiol-17β data indicate that there was a response to the additional hours in day length, at 38 wk of age, hens on 18L:6D had a higher concentration of circulating estradiol-17β than the hens on 14L:10D. A greater response may have occurred if the mid-cycle increase in day length was given at or before peak

egg production. This procedure would have minimized the effects of age on egg production, stimulating the flock before the decline in egg production began.

4. **Controlling BW and Increasing Flock Uniformity** Hurwitz and Bar (1971) noted that the change from pullet BW to adult BW occurred within a 2-wk period before the onset of lay. The photoperiod study (Joseph, Thesis: Chapter 4) demonstrated that during the pullet-to-breeder transition period there is a shift in the function of nutrient intake from growth to energy storage for reproduction. For example, as the hen aged, breast weight became proportionately smaller while abdominal fat pad weight became larger. Robinson et al. (1995) stressed that small differences in BW at the time of photostimulation can result in significant differences in energy requirements throughout lay. This means that a flock that is not uniform in BW will experience poor reproductive performance. Birds that are underweight coming into production will continue to partition nutrients that could be going into egg output into achieving a mature BW. Birds that are overweight will struggle to satisfy their maintenance requirements again, at the cost of egg production. One method of improving flock uniformity is to delay photostimulation to allow more birds to become physically mature (Hocking, 1996; Robinson et al., 1996). Robinson et al. (1996) noted that variability in BW in a flock decreased as age at photostimulation increased. In Experiment 2 (Joseph, Thesis: Chapter 3) delaying photostimulation resulted in a heavier BW at the time of photostimulation. Consequently, flock uniformity improved and the length of time between photostimulation and first oviposition was reduced by 15 d compared to hens photostimulated at 20 wk of age. In addition, hens photostimulated at 23 wk of age produced larger eggs and a similar number of settable eggs as hens that were photostimulated at 20 wk of age.

The Cobb 500 Breeder Management Guide states that early intake of protein can also lead to improved flock uniformity and it ensures the proper degree of fleshing on the bird (Anonymous, 1998). In Experiment 1, diets containing 16 and 18% CP did not increase BW or breast weight in hens. In a non-uniform flock, hens that are underweight may benefit from additional protein. Summers (1993) noted that a 17% CP prelay diet had positive effects on the reproductive performance of underweight Leghorn pullets. For hens that are overweight there is the possiblity that more protein could lead to excessive BW gain but Spratt and Leeson (1987) found that BW was influenced more by changes in energy rather than protein intake. Summers and Leeson (1994) observed that low-protein diets (i.e. 11 and 14% CP) resulted in underweight pullets that took longer to begin laying and laid smaller eggs. The present study demonstrated how important it is to ensure that rations contain the correct amount of dietary protein. A small reduction in the CP level (14 versus 16% CP) can have a significant impact on reproductive performance.

Currently the broiler industry is cost driven, that is, only the minimum levels of inputs are placed on the bird. Consequently, nutrition, environment, and disease control practices have been severly compromised (Emmerson, 2000). Genetic selection criteria for broiler breeders have shifted from meat yield and egg production to meat yield alone. That is, improved performance in growth rate has occurred at a cost to reproductive performance. Geneticists assure the poultry industry that the broiler has not yet reached its maximum performance in terms of growth rate. However realizing the genetic potential of the broiler can only occur under non-limiting genetic and environmental conditions. The broiler breeder hen has the potential for rapid growth but such growth would make her unfit for egg production. While feed restriction is a necessary practice to control BW gain, and with continued selection for growth and breast yield, the degree of restriction will have to increase. This then raises issues of physiological stress and animal welfare concerns (Mench and Falcone, 2000). The merging and elimination of primary breeder companies further complicate the problem as the number and diversity of genetic populations decrease. Therefore, further improvements in the broiler industry will have to depend on improving the performance of the bird by maximizing the inputs into production systems (Emmerson, 2000). Doing so will involve research that is focussed on improving the nutritional, environmental, and immunological status of the bird. The three experiments covered in this thesis demonstrated that genotype by environment interactions exist. A complete understanding of specific interactions would help the industry make significant improvements in management, nutrition, housing, and disease control in order to offset the impact that selection for growth has had on reproductive efficiency.

5.1 REFERENCES

Anonymous, 1998. The Cobb 500 Breeder Management Guide. Cobb-Vantress Inc., Siloam Springs, AR.

Emmerson, D., 2000. Evolving performance in the US broiler and turkey market. *in*: Proceedingsof the XXI World's Poultry Congress. Montreal, Canada.

Hocking, P. M., 1996. Role of body weight and food intake after photostimulatin on ovarian function at first egg in broiler breeder females. Br. Poult. Sci. 37:841-851.

Hocking, P. M., D. Waddington, M. A. Walker, and A. B. Gilbert, 1989. Control of the development of the ovarian follicular hierarchy in broiler breeder pullets by food restriction during rearing. Br. Poult. Sci. 30:167-174.

Hurwitz, S., and A. Bar, 1971. The effect of pre-laying mineral nutrition on the development, performance and mineral metabolism of pullets. Poultry Sci. 50:1044-1055.

Jaap, R. G., and F. V. Muir, 1968. Erratic oviposition and egg defects in broiler-type pullets. Poultry Sci. 47:417-423.

McDaniel, G. R., J. Brake, and M. K. Eckman, 1981. Factors affecting broiler breeder performance. 4. Interrelationship of some reproductive traits. Poultry Sci. 60:1792-1797.

Mench, J. A., and Falcone, C., 2000. Welfare concerns in feed-restricted meat-type poultry parent stocks. *in*: Proceedings of the XXI World's Poultry Congress. Montreal, Canada.

National Research Council, 1994. Nutrient Requirements of Poultry. 9th rev. ed. National Academy Press, Washington, DC.

Pearson, R. A., and K. M. Herron, 1981. Effects of energy and protein allowances during lay on the reproductive performance of broiler breeder hens. Br. Poult. Sci. 22:227-239.

Robinson, F. E., N. A. Robinson, and R. T. Hardin, 1995. The effects of 20-week body weight and feed allocation during early lay on female broiler breeders. J. Appl. Poultry Res. 4:203-210.

Robinson, F. E., T. A. Wautier, R. T. Hardin, N. A. Robinson, J. L. Wilson, M. Newcombe, and R. I. McKay, 1996. Effects of age at photostimulation on reproductive efficiency and carcass characteristics. 1. Broiler breeder hens. Can. J. Anim. Sci. 76:275-282.

Sharp, P. J., I. C. Dunn, and S. Cerolini, 1992. Neuroendocrine control of reduced persistence of egg-laying in domestic hens: evidence for the development of photorefractoriness. J. Reprod. Fertil. 94:221-235.

Spratt, R. S., and S. Leeson, 1987. Broiler breeder performance in response to diet protein and energy. Poultry Sci. 66:683-693.

Summers, J. D., 1993. Influence of prelay treatment and dietary protein level on the reproductive performance of White Leghorn hens. Poultry Sci. 72:1705-1713.

Summers, J. D., and S. Leeson, 1994. Laying hen performance as influenced by protein intake to sixteen weeks of age and body weight at point of lay. Poultry Sci. 73:495-501.

Waldroup, P. W., K. R. Hazen, W. D. Bussell, and Z. B. Johnson, 1976. Studies on the daily protein and amino acid needs of broiler breeder hens. Poultry Sci. 55:2342-2347.

Williams, J. B., and P. J. Sharp, 1978. Age-dependent change in the hypothalamo-pituitary-ovarian axis of the laying hen. J. Reprod. Fertil. 53:141-146.

Yu, M. W., F. E. Robinson, R. G. Charles, and R. Weingardt, 1992. Effect of feed allowance during rearing and breeding on female broiler breeders. 2. Ovarian morphology and production. Poultry Sci. 71:1750-1761.